TROPHIC ECOLOGY OF PIRANHAS (CHARACIDAE: SERRASALMINAE) FROM SAVANNA AND FOREST REGIONS IN THE ORINOCO RIVER BASIN OF VENEZUELA

By

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This study emphasizes interspecific and intraspecific comparisons of the trophic ecology of piranhas (Characidae: Serrasalminae) from two vegetatively distinct regions in the Orinoco River basin of Venezuela: (1) the upper Orinoco in the Federal Amazon Territory, an area dominated by dense tropical forests, and (2) the low Llanos of Apure State, a region characterized by immense open savannas. Eleven piranha species were taken from the two regions studied. Since 1979, ten species have been collected from the low Llanos of Apure State, whereas my 1989-1991 samples indicate that at least eight species occur in the upper Orinoco. Seven species were widely distributed and inhabited both regions. The high similarity in species composition between the two regions suggests that there are really no distinct savanna versus forest piranha assemblages.

All piranhas exhibit changes in diet with age. The smallest juveniles, < 20 mm standard length (SL), prey mainly on microcrustaceans and small aquatic insects. Older juveniles of most species, between 20 and 80 mm SL, commonly eat fins. Fin eating by

young piranhas is common in both the low Llanos and the upper Orinoco. Chemical analysis indicated that fins are similar to scales in energy and protein content, but less than that of small whole fish. Orinoco piranhas ≥ 80 mm SL fall into two general dietary categories: species that are primarily carnivorous and others that are largely herbivorous. The seven carnivorous piranhas (*Pygocentrus caribe*, *Serrasalmus altuvei*, *S. manueli*, *S. rhombeus*, *S. elongatus*, *S. irritans*, and *S. medinai*) feed heavily on fish or fish fins. Adults of the four herbivorous species (*Serrasalmus* cf. *eigenmanni*, *Pygopristis denticulatus*, and two *Pristobrycon* spp.) are seed predators, biting seeds and hard fruits into small fragments before ingesting them. *Serrasalmus manueli* was one of the few carnivorous species that occasionally took seeds or fruit in mass. Overall, relative intestine length differed among serrasalmine species and was closely correlated with diet. Seed-eating piranhas tended to have long intestines, similar to those of highly herbivorous *Myleus*, *Mylossoma*, and *Metynnis* species, but I found no significant difference in relative intestine lengths between forest and savanna populations of *S. manueli* even though diets differed.

Both carnivorous and herbivorous species are somewhat flexible in their use of food resources. I found that upper Orinoco piranhas, at both the group and species levels, exploit plant material more than piranhas from the low Llanos. Many piranhas, especially those that are largely herbivorous, shift their diets in response to spatial as well as temporal variation in the availability of fish prey versus plant food. Even though savanna and forest regions have a similar piranha species makeup, herbivorous species are much more common in forested regions. Nevertheless, even though seeds and fruits are a locally abundant resource, assemblages of forest piranhas were typically dominated by one or two large, highly carnivorous species (*S. rhombeus*, *S. manueli*, or both).

CHAPTER 1
INTRODUCTION

Introduction to Piranhas

Piranhas (Characidae: Serrasalminae) are neotropical freshwater fishes found in the major Atlantic drainages of South America, from 10° North latitude in the Orinoco River basin of Venezuela and Colombia, through the Amazon basin, and south in the La Plata-Paraguay-Parana basin to about 35° South latitude. Called caribes in Venezuela, they comprise a monophyletic group of at least 30 species in the genera *Serrasalmus*, *Pygocentrus*, *Pristobrycon* and *Pygopristis* (Fig. 1-1) (Machado-Allison 1983, 1985, Fink 1988). Piranhas possess many unique morphological traits that distinguish them from other serrasalmines (Machado-Allison 1985), but they are most easily recognized by their unusual and impressive dentition. They have a single row of sharp, somewhat triangular teeth in both jaws; the teeth are tightly packed, partially interlocking, and are typically used for rapid puncture and shearing.

Examples of other serrasalmine fishes are species of *Mylossoma*, *Myleus*, and *Metynnis* (silver dollars, *pámpanos*, *palometas*), the scale-eating characin *Catoprion mento*, and the nearly one-meter long *Piaractus brachypomus* (*morocoto*) and *Colossoma macropomum* (*cachama* or *tambaqui*). In contrast to the piranhas, the dental morphologies of other serrasalmine fishes are variable. Most species have combinations of relatively broad and strong molariform and incisive teeth, often with more than one row of teeth in the upper jaw. Serrasalmine fishes are laterally compressed and most are fairly deep-bodied; however, maximum adult size, body shape, and color patterns vary among species. Piranhas range from medium-sized fishes such as *Serrasalmus irritans*, some 20 cm from

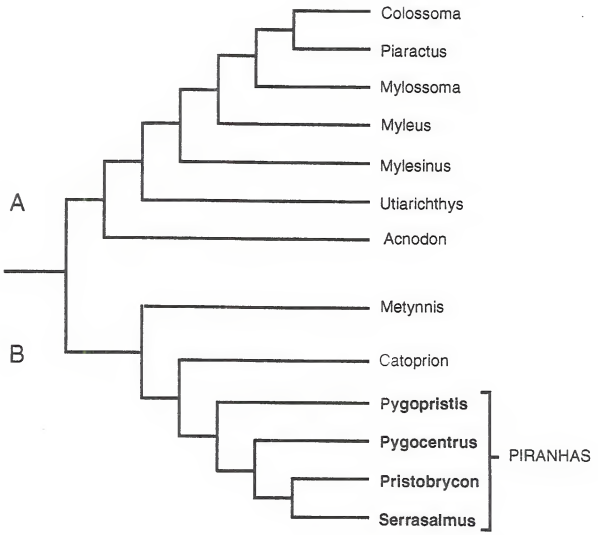


Fig. 1-1. Hypothesized phylogenetic relationships among genera of the subfamily Serrasalminae as proposed by Machado-Allison (redrawn from Machado-Allison 1985).

tip of snout to base of tail (Standard Length, SL) to large species such as *Serrasalmus rhombeus*, which grow to well over 35 cm SL. The general body form ranges from sharp-snouted and elongate, *Serrasalmus elongatus*, to blunt-headed and robust species such as the red-bellied piranhas *Pygocentrus caribe* of the Orinoco and *P. nattereri* of the Amazon.

Of the approximately thirty species of piranhas, at least twelve occur in the Orinoco basin where, as in many other areas of tropical South America, they are exploited for subsistence fisheries and also commercially. Piranhas occur in rivers and floodplains of both open savannas and densely forested regions and often make up a high percentage of fish biomass and numbers of individuals (Mago-Leccia 1970, Taphorn and Lilyestrom 1984). Thus, they play a major role in the food web of many lowland aquatic communities. Contrary to common belief that they are strictly carnivorous, piranhas and their close relatives exploit a broad spectrum of food resources including arthropods, fishes and other vertebrates, fish fins and scales, carrion, seeds, fruits, leaves, and flowers (Goulding 1980, Sazima 1983, Sazima and Guimarães 1987, Nico and Taphorn 1988, Winemiller 1989a, Sazima and Machado 1990). Serrasalmine fishes living in tropical savannas encounter substantially different habitat conditions in comparison to those populations occupying forested regions. Thus, comparative studies of piranha diets and trophic ecology can provide insights into their responses and adaptations to the selective forces of different environments

Purpose of Present Study

Tropical South America possesses the most diverse freshwater fish fauna of any continent (Böhlke et al. 1978). Considering both described and undescribed taxa, Lundberg et al. (1987) estimated that the Orinoco River basin alone probably contains almost 1,000 fish species, more species than are found in all the freshwater systems of temperate North America. Unfortunately, the extremely diverse faunas and floras of many

tropical environments are seriously threatened. Because of expanding human populations and increased development, natural habitats are being destroyed or degraded at a rapid pace. Forests are being cleared for agriculture, ranching, timber, and minerals; rivers and their floodplains are being modified by dams, levees, and pollution. Aquatic and terrestrial systems in the lowland tropics are intricately interwoven, the changes to each inevitably affecting the other. The profound and likely irreversible changes now occurring throughout tropical America make it increasingly important to understand more about the interrelationships between tropical environments and their diverse fauna and flora. Such an understanding is necessary for successful conservation of habitats, species, and genetic stocks.

The science of ecology attempts to understand the complex interrelationships between an organism and its physical and biotic environment. Studies in trophic ecology are a way to investigate such interrelationships, and often permit analysis at several levels or scales. Obviously, what an animal eats is limited by the kinds and availability of food resources in its local surroundings. Valid interpretations of feeding patterns, however, also require consideration of past environmental conditions, inasmuch as the probability of an animal taking a particular type of prey depends on its array of interrelated morphological and behavioral characters that result from its particular phylogenetic history. Trophic studies provide insights into the biology of organisms, because food, unlike many other resources or niche parameters, can be measured, analyzed, and compared in a large number of ways using a variety of techniques. Evidence for the importance and practicality of research on trophic ecology is provided by the tremendous volume of literature on the subject (for review of fishes see Ross 1986). Accordingly, the study of diets and food resources has contributed to the development of many ecological concepts, including resource partitioning, niche theory, optimality theory, energetics, food webs, and predator-prey relationships.

The aim of this study is to increase our knowledge of the ecology and natural history of piranhas and a few of their close relatives. I have attempted to document and explain similarities and differences in trophic ecology within and among closely related species by comparing populations from two floristically distinct regions of the Orinoco River Basin of Venezuela: (1) the upper Orinoco, an area dominated by dense forests, and (2) the low Llanos of Apure State, a region characterized by immense open savannas.

Piranhas are widely distributed geographically and very abundant in many lowland tropical habitats, but we know relatively little about their ecology, behavior, and natural history. Goulding (1980) found many fishes in the Amazonian forest ecosystems, including several piranhas, to be herbivorous or omnivorous and to depend heavily on flooded forests for food resources. Influenced by Goulding's findings, Donald Taphorn and I began, in late 1983, to study the trophic ecology and natural history of piranhas and other fishes in savanna ecosystems of the Venezuelan Llanos (Nico and Taphorn 1988, Nico 1990). Although my initial research on piranhas focused on savanna regions in the Orinoco Basin, I also made visits to southern Venezuela and the Rio Casiquiare in 1985, and to Marajó Island in the lower Amazon of Brazil in 1986. Subsequently, between May 1988 and March 1991, I participated in five expeditions to the upper Orinoco basin and its forests to broaden my investigation of the feeding ecology of Orinoco piranhas as related to their habitat.

Waters of the low Llanos are typically high in fish and invertebrate biomass, and many sites support large numbers of carnivores (Mago-Leccia 1970, Taphorn and Lilyestrom 1984, Machado-Allison 1987, Saunders and Lewis 1988, Rodríguez and Lewis 1990). However, large woody plants are uncommon, and in conjunction with water stress caused by the yearly dry periods, production of seeds and fruits is highly seasonal (Sarmiento 1984). As a result, availability of plant materials, especially fruits and large seeds, as food for savanna fishes is low, markedly seasonal, and very localized (personal observations). On the other hand, the few phenological studies of wet forests in lowland

areas of tropical South America (Terborgh 1983, Goulding et al. 1988, Janson and Emmons 1990), or information gleaned from botanical exploration of the upper Orinoco (B. Stergios, personal communication), suggest that such habitats make a wide variety and abundance of fruits and seeds available to fishes during most of the year (Goulding 1980, Goulding et al. 1988). Even though species diversity is often high in the upper Orinoco, our collections made with a variety of fishing gear indicate that fish biomass in tropical forest regions is generally lower than in the low Llanos.

If present ecological conditions are important, environment should strongly influence both species composition and trophic ecology of piranha assemblages in particular regions. Accordingly, comparisons of piranhas from the more heavily forested upper Orinoco basin with those from the open savannas or low Llanos were made to address the following questions: (1) Do the same species of piranhas occur in both savanna and forested regions? (2) Do diets differ, and, if so, are fish from populations in forested habitats significantly more herbivorous than their savanna counterparts? (3) Do ontogenetic shifts in diet occur and, if so, how do they compare among species and do they correlate with regional environments? (4) Because gut length is often an indicator of natural diet in vertebrates (i.e., longer in herbivores), is intestinal length of piranhas and other serrasalmine fishes correlated with diet? (5) What are the nutritional benefits associated with different diets or food preferences (e.g., scale- or fin-eating versus flesh-eating)? (6) How do diets of piranhas compare with other serrasalmine species? (7) What is the relationship between piranha ecology and serrasalmine phylogeny?

The comparative approach is useful in helping us understand aspects of the evolution and adaptations of closely related species (Clutton-Brock and Harvey 1984, Huey and Bennett 1986). Recent comparative studies in tropical vertebrate ecology have focused on birds (Schluter 1988), mammals (Terborgh 1983), and reptiles and amphibians (Duellman 1990). An objective in many comparative studies is discovery of evolutionary trends in morphological and behavioral adaptations to different environments, thereby

making it possible to recognize how particular characters arise under the influence of contrasting selective forces (Clutton-Brock and Harvey 1984). Furthermore, comparisons across a broad biogeographical scale offer what Wiens et al. (1986) suggested as perhaps the best opportunity to understand a species' limits or responses to different environmental conditions, revealing patterns that suggest something of its adaptive abilities or evolutionary potential.

Literature Review

The following is a brief review of the literature relating to piranha feeding behavior and trophic ecology. A summary of field studies investigating piranha feeding and diets is given in Table 1-1. Unless otherwise stated, scientific names are as used in the original literature. All references to *Serrasalmus nattereri* should be *Pygocentrus nattereri*.

Early naturalists and explorers were the first to report on piranhas, and most accounts, such as those by Alexander von Humboldt, Henry Bates, and Theodore Roosevelt, were primarily devoted to describing attacks by piranhas on animals and humans, or relating the destruction done by piranhas to fishing gear (Bates [1863] 1975:202, Roosevelt 1914). Humboldt, who traveled extensively in South America between 1799 and 1804, wrote the following passage while on the Orinoco River:

> On the morning of the 3rd of April our Indians caught with a hook the fish known in the country by the name of *caribe** [**Caribe* in the Spanish language signifies *cannibal*], or *caribito*, because no other fish has such a thirst for blood. It attacks bathers and swimmers, from whom it often bites away considerable pieces of flesh. The Indians dread extremely these caribes; and several of them showed us the scars of deep wounds in the calf of the leg and in the thigh, made by these little animals. They swim at the bottom of rivers; but if a few drops of blood be shed on the water, they rise by thousands to the surface, so that if a person be only slightly bitten, it is difficult for him to get out of the water without receiving a severer wound.
> Humboldt ([1816-1831] 1971:166-167)

Eigenmann (1915), Eigenmann and Allen (1942), and Myers (1972) have reviewed many of the earlier stories about piranhas. Although published anecdotal information brought notoriety to this group of South American fishes, early accounts did not significantly contribute to our knowledge of piranha biology and natural history, and many stories simply aided to perpetuate myths about piranha ferocity.

There have been a moderate number of studies that have addressed the natural diets of piranhas (Table 1-1). Most of these have focused on only one or a few of the most common and widespread species, from a single locality or region. The diets of several of the more uncommon species have never been described. Most studies of piranha diets have been of fishes inhabiting artificially altered environments. Because a few of the more common piranha species seem to flourish in man-made lakes, several studies focused on populations inhabiting reservoirs or impoundments. Work on piranhas has also been done in watersheds modified to some extent by cattle ranching, agriculture, and by construction of roadways. Few investigations have been carried out in pristine habitats.

Several of the earliest efforts to characterize piranha diets were carried out in the Jaguaribe River basin, a coastal drainage located in northeastern Brazil. The first was that of Menezes and Menezes (1946). Along with information on several other species, they presented a simple listing of food items, primarily fish remains and insects, found in the stomachs of 138 specimens of a single piranha species taken in 1944 from the Lima Campos Reservoir in Ceará State. First identified by Menezes and Menezes as *Serrasalmo immaculatus*, Braga (1954) later indicated the species was *Serrasalmus rhombeus*. Braga also studied Lima Campos piranhas. He recorded the frequency of occurrence and volume of stomach contents of a large sample of *S. rhombeus* (n = 2,222; 100-290 mm total length) during a 12-month study, 1952-1953 (Braga 1954). Of the 1,713 individuals containing food, predominant food items were freshwater shrimp (Palaemonidae) and fish, 65 and 28 percent of the total food volume, respectively. Braga later published results from other studies on piranhas in a single volume (Braga 1975), providing diet information

Table 1-1. Summary of principal field studies investigating piranha feeding and diets in order of publication date. All studies based on analysis of stomach contents unless otherwise indicated. Most measured size as standard length in mm, if not, size given as total length (TL) or weight in grams (g). Scientific names are as used in original literature unless marked with asterisk (*) (also see nomenclatural changes discussed in Chapter 3).

Basin (State, Country)	Site or Habitat	Study Period and Duration	Species	No. Examined (Size range)	Comments	Source
1. Jaguaribe (Ceará, Brazil)	Lima Campos Reservoir	1944, May to October	1) *Serrasalmo immaculatus* (=*Serrasalmus rhombeus*)	n = 138 (wt: 10–215 g)	Diet consisted mainly of fish remains	Menezes and Menezes (1946)
2. Jaguaribe (Ceará, Brazil)	Lima Campos Reservoir	12-month study, 1952-1953	1) *Serrasalmus rhombeus*	n = 2,222 (100-290 TL)	Fed mainly on shrimp and fish	Braga (1954)
3. Essequibo and Amazon (Guyana)	Rupununi Savanna, savanna pools	Intermittent 1957, 1958, and 1961 (~2 months total)	1) *Serrasalmus nattereri*, 2) *S. rhombeus* 3) *S. gymnogenys* 4) *Pygopristis denticulatus*	Number examined not given	Reduced feeding found during dry season	Lowe-McConnell (1964)
4. Paraná (Argentina)	Middle Paraná rivers, lagoons (?)	Intermittent 1962 to 1966	1) *Serrasalmus spilopleura* 2) *S. nattereri*	n = 104 (3-657 g) n = 21 (10–200 g)	Diet of mostly fish	Bonetto et al. (1967)
5. Amazon (Pará, Brazil)	Three sites: Lago Jacupá, no data on other two	1967 (?)	1) *Serrasalmus elongatus*	n = 7 (89-152)	All contained fins, some scales; fins major item in all but two	Roberts (1970)
6. Jaguaribe (Ceará, Brazil)	Three reservoirs: Roque de Macêdo, Cruzeiro do Sul, Assis Machado	Intermittent 1970-1972: Nov. 1970, May 1972, other date?	1) *Serrasalmus nattereri*	n = 500 (125-370 TL)	Fed mainly on fish (small characins)	Braga (1975)
7. Napo-Amazon (Ecuador)	Rio Aguarico floodplain lakes, side channels	Intermittent 1967 and 1968 (~3 1/2 months)	1) *Serrasalmus nattereri* 2) *S. marginatus*	n = 6 (30-321) n = 4 (45-224)	1) fish remains and insects 2) fish remains	Saul (1975)

Table 1-1--continued.

Basin (State, Country)	Site or Habitat	Study Period and Duration	Species	No. Examined (Size range)	Comments	Source
8. Amazon (Amazonas, Brazil)	Madeira River drainage Rio Machado (rivers, flooded forest)	1977 and 1978 high and low water; 1979 high water	1) *Serrasalmus rhombeus* 2) *S. elongatus* 3) *S. serrulatus* 4) *S.* cf.*striolatus* 5-7) *Serrasalmus* spp.	n = 254 (180-370) n = 67? (140-220) n = 36 (130-250) n = 9 (150-200) n = 5? (no data)	Adults of some species highly carnivorous, other species feed on seeds and fruits; concluded all or many omnivorous	Goulding (1980)
9. Tietê River (São Paulo, Brazil)	Bariri Reservoir	Sampled four seasons of year, Jan. to Dec. 1979	1) *Serrasalmus spilopleura*	n = 299 (75-295 TL)	Study of seasonal changes in average stomach fullness, heaviest feeding in Summer.	Mota et al. (1982)
10. Atibaia River (São Paulo, Brazil)	Americana Resevoir	Feb. to Apr. 1983	1) *Serrasalmus spilopleura*	n = 41 (10.5-19.5)	Stomach contents of larval and small juveniles, feeding behavior of juveniles in aquaria	Sazima and Zamprogno. (1985).
11. Amazon (Pará, Brazil)	Curuá-Una Reservoir	Three collections, Aug., Nov., 1982 Feb. 1983	1) *Serrasalmus rhombeus*	n = 250 (50-320)	Compared diets among five sites in reservoir, mainly fed on fish, one site aquatic insects	Ferreira (1984b, also see 1984a)
12. Orinoco (Guarico, Venezuela)	Apure drainage savanna lagoon	Intermittent 1982-1984 wet seasons	1) *Pygocentrus notatus* 2) *Serrasalmus rhombeus* 3) *Pristobrycon striolatus*	n = 44 (10–100) n = 50 (10–100) n = 40 (10–100)	Juvenile diets, smallest fed on microcrustaceans; larger ate fins, scales, fish flesh, small seeds	Machado-Allison and Garcia (1986)
13. Paraná (São Paulo Brazil)	Tietê drainage Americana Reservoir of Atabaia River,	Intermittent 1982 to 1984	1) *Serrasalmus spilopleura*	n = 115? (10–207)	Diet mainly fins, scales, fish flesh, and whole fish	Northcote et al. (1986, 1987)
14. Paraná (Mato Grosso, Brazil)	Pantanal region	1985 and 1986	1) *Pygocentrus nattereri* 2) *Serrasalmus spilopleura*	Not applicable	Investigated three reported cases of piranhas scavenging on human corpses	Sazima and Guimarães (1987)

Table 1-1--continued.

Basin (State, Country)	Site Habitat	Study Period and Duration	Species	No. Examined (Size range)	Comments	Source
15. Orinoco (Apure, Venezuela)	Apure drainage, savanna streams, pools, flooded savanna; cattle ranch	Intermittent from 1979 to 1986, all months sampled	1) *Pygocentrus caribe** 2) *Serrasalmus medinai** 3) *S. irritans* 4) *S. rhombeus* 5) *S. elongatus* 6) *S. altuvei* 7) *Pristobrycon striolatus* Unidentified juveniles	n = 516 (20-280) n = 124 (31-150) n = 271 (22-162) n = 51 (20-235) n = 42 (23-175) n = 10 (55-155) n = 16 (21-159) n = 114 (10-19)	Ontogenetic changes in diet, smallest fed on microcrustaceans, most large juveniles ate fins, adults were mainly piscivores. Plant material not important in diet (see Chapter 5)	Nico and Taphorn (1988) (see Chapter 5)
16. Amazon (Amazonas, Brazil)	lower Rio Negro beaches, lakes, swamps, flooded forest	Intermittent 1979 to 1987	Six piranha species (not identified)	n = 392 ? (size range not given)	Part of larger study, piranhas fed on fish and plant matter	Goulding et al. (1988)
17. Orinoco (Portuguesa, Venezuela)	Apure drainage small seasonal stream; cattle ranch	~12-month 1984	1) *Pygocentrus caribe** 2) *Serrasalmus medinai** 3) *Serrasalmus rhombeus* 4) *Serrasalmus irritanss*	n = 230 (20~200) n = 68 (20~80) n = 50 (20~200) n = 76 (20~150)	Piranhas taken 8 of the 12 months, mostly juveniles. Ontogenetic changes in diet documented	Winemiller (1989a)
18. Paraná (Mato Grosso, Brazil)	Pantanal region Paraguai drainage clearwater pools and creeks:	Intermittent from 1981 to 1989, mostly during wet season	1) *Serrasalmus marginatus* 2) *S. spilopleura* 3) *Pygocentrus nattereri*,	n = 13 (63-146) n = 26 (64-160) n = 24 (80-240)	Stomach contents presented and detailed underwater observations totalling 314 hours	Sazima and Machado (1990)
19. Orinoco (Apure, Venezuela)	Apure drainage small seasonal stream; cattle ranch	24-hour period, August 4-5, 1988 wet season	1) *Pygocentrus caribe**	n = 123 (40-68)	24-hour diel study of juvenile feeding; fed mostly on small fish and aquatic insects, peak feeding in morning	Nico (1990)

on *S. nattereri* from three other reservoirs of the Jaguaribe basin. In that work, Braga concluded that piranhas were carnivorous, preferring to feed on other fishes, although they also prey on other vertebrates (i.e., birds and amphibians), some invertebrates, and only occasionally on plant material, such as seeds, parts of leaves, and algae.

Bonetto et al. (1967) reported on the feeding habits of two piranhas, *Serrasalmus spilopleura* (n = 104) and *S. nattereri* (n = 21), taken from the middle Paraná River and its floodplain in Argentina. Both species fed predominantly on fish, but prey were not identified to lower taxa. Stomachs of many of the individuals examined contained small amounts of plant material, for example, roots and leaves of the aquatic plant *Salvinia* sp. and roots of *Eichhornia* sp. (water hyacinth); however, these items were thought to have been taken accidentally during capture of their principle prey.

Lowe-McConnell (1964) studied the ecology of fishes in the Rupununi savanna of the Essequibo River basin, British Guiana (present day Guyana). Although not focusing on fish diets, she briefly mentioned that the stomachs of fishes trapped in drying pools, including the piranhas *Serrasalmus nattereri*, *S. rhombeus*, and *Pygopristis denticulatus*, contained only mud and bottom debris; however, these same fishes had large amounts of body fat. From her work in the Essequibo River drainage, Lowe-McConnell concluded that the dry season was a period when fishes exhibited reduced feeding and high diet overlap.

Roberts (1970) was the first to report on the more unusual feeding practices of piranhas when he found large amounts of fins and some scales in the stomachs of seven *Serrasalmus elongatus* from several sites in the Amazon River basin. He also discussed scale-eating by the serrasalmine *Catoprion mento*. Saul (1975) collected two piranha species during his study of habitat and food preferences of fishes at a site along the Aguarico River, a tributary of the Napo River in the western Amazon Basin, Ecuador. He found the stomachs of *Serrasalmus nattereri* (n = 6) to contain fish remains and insects;

those of *S. marginatus* (n = 4) held fish and fish remains. Both species were found primarily in floodplain lakes or side channels, as opposed to the main river.

The relationship between piranha feeding patterns and environment had not been investigated in any detail, however, until Goulding (1980) studied the diets of medium and large-sized adult fishes, including seven piranha species, from in and around the Machado River, a clearwater tributary of the turbid-water Madeira River in Amazonia Brazil, a region of seasonally inundated forests. He found that large *Serrasalmus rhombeus* (n = 254), the most common piranha taken, were primarily piscivores that often bit chunks of flesh out of large fish. Of added interest, fruits and seeds made up an estimated 10 percent of the total volume of food eaten by *S. rhombeus*. Adult *S. elongatus* (n = 85) collected by Goulding were similar to the juveniles examined by Roberts in that they had fed heavily on fins and scales. Goulding reported that five of the seven species fed heavily on seeds, which they masticated before swallowing. These five piranhas, which were relatively uncommon in samples, included *Serrasalmus serrulatus* (n = 36), *Serrasalmus* cf. *striolatus (n = 9)*, and three unidentified *Serrasalmus* species (n = 5?). Goulding concluded that Amazonian fishes had evolved a close interrelationship with lowland forests, and that many fishes depended on flooded forests for food in the form of fruit, seeds, and other allochthonous materials. In addition to being seed predators, Goulding (1983) later indicated that piranhas sometimes took seeds whole, and suggested that these fish also acted in dispersal of seeds.

After Goulding completed his work in the Madeira River basin, he was joined by Carvalho and Ferreira (Goulding et al. 1988) in a study on the natural history of Amazonian fishes in habitats associated with the main channel of the lower Rio Negro. Of approximately 450 species taken in the Rio Negro, six were piranhas. They did not discuss piranha diets in much detail, but reported that fin and scale eating by adult piranhas seemed to be common. Their collections of juvenile piranhas from the Rio Negro are yet to

be analyzed. In the published proceedings of a symposium Leão et al. (1989) reported on the morphology, reproduction, and diet of *Serrasalmus altuvei* from the Rio Negro.

Sazima and his colleagues have explored the behavior of piranhas and related species, particularly in reference to fin and scale-eating, through laboratory work with captive fishes and underwater observations of free-living fishes in the Pantanal region, western Brazil (Sazima 1983, 1986, 1988; Sazima and Zamprogno 1985, Sazima and Pombal 1988, Sazima and Machado 1990). Sazima and Guimarães (1987) recognized *Pygocentrus nattereri* and *Serrasalmus spilopleura* as scavengers, feeding on dead and sometimes decaying fishes, birds, and mammals. They suggested that deaths of humans attributed to piranhas might often be the result of scavenging on victims already dead from drowning or other causes. Sazima and Machado (1990) presented data from their underwater observations on the behavior of three species, *S. marginatus*, *S. spilopleura*, and *P. nattereri*, with emphasis on their predatory tactics, feeding behavior, and social interactions while foraging.

Ferreira (1984b) studied the food and feeding habits of the principal fish species inhabiting the Curuá-Una River Reservoir, in the Amazon Basin near Santarém, Brazil. Ferreira found that the diet of *Serrasalmus rhombeus*, taken from five localities in the reservoir, showed slight differences among stations, feeding mainly on fish at four sites, and on aquatic insects (i.e., ephemeroptera) at a fifth locality. In total, 250 specimens were examined (ranging from 50 to 320 mm SL) of which 196 piranhas contained food.

Northcote et al. (1986, 1987) reported fin feeding by *Serrasalmus spilopleura* from the Americana Reservoir, an impoundment on the Atibaia River in southeastern Brazil. Analysis of prey fishes with damaged fins showed that *S. spilopleura* usually nip the lower lobe of fins, indicating that attacks are made from below and behind prey fishes. They also suggested that *S. splilopleura* was the main, if not the only, fin-feeder in the reservoir fish community. Mota et al. (1982) studied the seasonal variation in the intensity of feeding, as measured by stomach fullness, of *S. spilopleura* from the Bariri Reservoir in São Paulo

State, Brazil. They reported that heaviest feeding took place during the summer months with a corresponding heavy build up of body fat by autumn.

Several recent works dealing with piranhas in the Venezuelan Llanos have documented diet shifts during ontogeny (Machado-Allison and Garcia 1986, Nico and Taphorn 1988, and Winemiller 1989a). All found that early juveniles ate principally zooplankton, while older individuals were predominantly piscivores. In addition to discussing ontogenetic changes in dental morphologies, Machado-Allison and Garcia (1986) examined 134 specimens, mostly juveniles, of three species (*Pygocentrus caribe Pristobrycon striolatus*, and *Serrasalmus rhombeus*) taken from the Camaguán lagoon, a large wetland between the Portuguesa and Apure rivers, Guarico State. Predominant food items, in terms of frequency of occurrence, of young piranhas were microcrustaceans, aquatic insects, fins, and scales. In addition, they found small seeds (i.e., Cyperaceae) in the stomachs of 33 of 134 specimens, but did not provide information on volume and numbers of seeds eaten. Nico and Taphorn (1988) examined the diets of seven piranha species from streams and flooded savannas in the western Llanos of the Orinoco River Basin. Their work suggested that savanna piranhas do not depend on fruits and seeds as had been reported by Goulding (1980) for piranhas in flooded tropical rain forests. Nico and Taphorn found that juveniles and sub-adults of six of seven piranhas from a single locality fed heavily on fins. Winemiller (1989a) studied the fish community of Caño Maraca, a seasonal stream in the Apure River drainage that meanders through a region of wooded savannas used for cattle ranching and cropland in Portuguesa State. His findings on four piranha species (*P. caribe*, *S. irritans*, *S. rhombeus*, and *S. medinai*), mostly juveniles and sub-adults, supported the earlier work of Nico and Taphorn.

For the most part, piranhas have been found to be daytime feeders, usually most active during twilight periods (Lowe-McConnell 1964, Goulding 1980, Barthem 1987, Nico 1990, personal observations). Barthem (1987) reported on activity patterns of several várzea lake fishes from near Manaus, Brazil. His results, based on analysis of gillnet

catches, suggest an early morning peak of activity in *Pygocentrus nattereri*, *Serrasalmus elongatus*, and *S. rhombeus*, and a late afternoon peak for the latter two species. Nico (1990) found that young *Pygocentrus notatus* (= *P. caribe*) had a peak feeding activity in the morning, whereas adults seemed to be more active near dusk.

Intestine length of a few piranha species has been measured by Braga (1954), Luengo (1965), Bonetto et al. (1967), and Jégu and dos Santos (1988). Braga reported that the digestive tract of *Serrasalmus rhombeus* averaged 1.4 times the standard length. Luengo (1965), relating intestine length to natural diet, reported that the highly carnivorous *Serrasalmus nattereri* (= *Pygocentrus caribe*) taken in the Venezuelan Llanos had a short intestine compared with that of *Prochilodus reticulatus* (= *Prochilodus mariae*?), a prochilodid fish that feeds primarily on organic mud and detritus. Martínez (1976:67) studied the anatomy of what was identified as *Serrasalmus nattereri* (= *Pygocentrus caribe*) and reported 10 to 12 intestinal caeca originating near and slightly past the pylorus. In a taxonomic treatment, Jégu and dos Santos (1988) provided information on intestine length and number of pyloric caeca for several piranha species from the Rio Tocantins of Brazil, but they did not suggest dietary correlations.

Organization of Dissertation

The content and sequence of the chapters reflect the major components of my study. Chapter 2 provides an overview of the Orinoco River basin and describes the environment of the two study regions. Chapter 3 identifies the study sites and details field and laboratory methods used. Chapter 4 compares the species composition of piranha assemblages between the two regions and among the different drainages. Chapter 5 presents results from long-term studies on the trophic ecology and natural history of savanna populations of piranhas from a site in the Apure River drainage. Chapter 6 focuses on the trophic ecology of populations of serrasalmine fishes from six drainages in

the upper Orinoco River Basin, a region characterized by extensive forests that undergo seasonal flooding. In addition, my findings from the upper Orinoco are compared to results from my studies of savanna populations, including data on a few savanna species not reported in previous studies. Chapter 7 then gives results of an analysis of the nutritive values of various food items commonly taken by piranhas. Finally, Chapter 8 summarizes the major findings of the study, and attempts to interpret and synthesize the results in terms of relevant mechanistic, ecological, and evolutionary issues.

CHAPTER 2
THE ENVIRONMENTAL SETTING

In this chapter I give an overview of the Orinoco River basin and describe the two regions dealt with in the present study: (1) the open savannas or low Llanos of Apure State, and (2) the upper Orinoco in the Venezuelan Federal Territory of Amazonas, an area dominated by forests. Little is known about the geological and ecological history of tropical lowlands in South America (Whitmore and Prance 1987). Because historical events undoubtedly influenced present-day ecological patterns, I briefly review several hypotheses concerning the basin's and the river's formation, as well as climatic and vegetation changes that purportedly took place in northern South America during the recent past.

The Orinoco River Basin

The Orinoco River, although dwarfed by the Amazon, is a major tropical river. The basin is located in northern South America between 2° and 10° N latitude, and empties into the Atlantic Ocean (Fig. 2-1). The Orinoco's mean annual discharge is about 35,800 m^3/sec from a drainage area of approximately 1,100,000 km^2, located in Venezuela (70%) and Colombia (30%) (Lewis 1988). Compared to the Mississippi River, the Orinoco has more than twice the annual discharge, yet drains an area of only one-third the size. The basin is geologically and ecologically diverse, having large mountain ranges and broad low-lying plains, with habitats ranging from immense open grasslands to lush tropical forests.

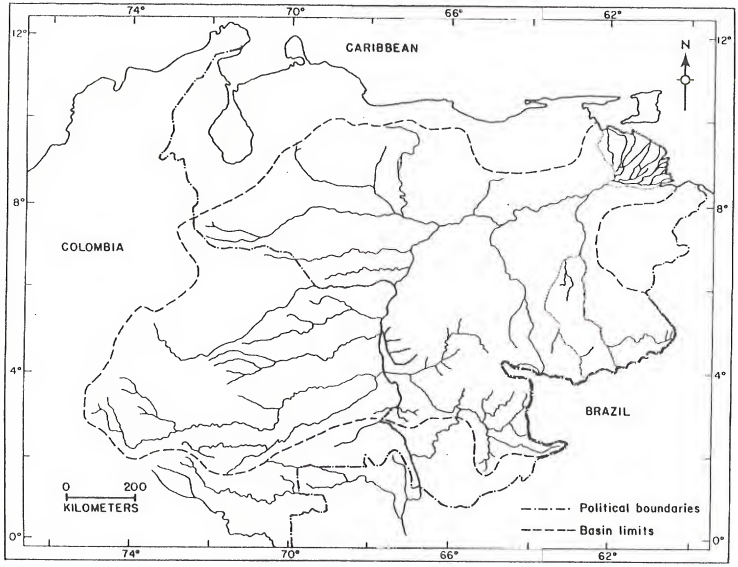


Fig. 2-1. Map of northern South America showing Orinoco River basin.

The headwaters of the Orinoco are traditionally considered to be in southern Venezuela where it receives water from both the western slopes of the Guyana Shield and from extensive lowland areas dominated by deciduous or evergreen tropical forest. In contrast, most tributaries in the northern and western parts of the basin originate in the Andes and adjoining coastal mountains and then flow through the Llanos, a vast alluvial plain supporting tropical savanna vegetation. The main channel of the Orinoco forms an unusual U-shaped pattern, the river winding around the western borders of the Guyana Shield. From its source the Orinoco flows several hundred kilometers west-northwest until it is met by the Atabapo and Guaviare rivers; here the river makes an abrupt turn to the north. Along its northward segment the Orinoco forms the border between Colombia and Venezuela.

At about 5°30'N latitude the river courses through several series of treacherous cataracts near Puerto Ayacucho, the most prominent being the Atures Rapids where the river drops 17.5 m over a distance of 9.3 km (CODESUR 1979). The Atures Rapids and the other cataracts are spread along a reach of nearly 100 km, marking the boundary between the upper and lower sections of the Orinoco. Farther downstream the Orinoco is joined from the west by the Meta, Cinaruco, Capanaparo, and Apure rivers as it gradually swings to the east. Finally, below the confluences with the Caura and Caroni rivers the Orinoco arrives at its large delta. Here the huge main river is subdivided into a multitude of smaller channels that empty into the Atlantic Ocean near the island of Trinidad. The main causeway of the Orinoco, from its origin in the Sierra Parima in the Guyana Shield to its mouth, is estimated to be 2,140 km long (DISCOLAR 1983). High-order tributaries draining highland areas of the Andes and the Guyana Shield are characterized by large numbers of waterfalls, rapids, and fast-flowing waters. However, the larger streams and rivers common to lowland areas typically have slight gradients. The upper Orinoco, at the

community of La Esmeralda, nearly 1,800 km by river from the sea, is only 135 m above sea level, an average drop of less than 1 m for every 10 km of river.

In summary, large rivers of lowland forests that feed the upper Orinoco from the south include the Mavaca and Atabapo rivers. Big-river tributaries originating in the Guyana Shield and feeding into the upper Orinoco include the Ocamo, Padamo, Cunucunuma, Ventuari, and Sipapo; those flowing into the lower Orinoco include the Caura and Caroni rivers. Large tributaries of the Orinoco that originate on or near the Andean slopes are the Inirida, Guaviare, Vichada, Tomo, Meta, Cinaruco, Capanaparo, Arauca, and Apure rivers. About 31 percent of the upper Orinoco volume is continually diverted into the Amazon basin by way of the Brazo Casiquiare, a natural canal (CODESUR 1979).

In addition to a diverse flora and topography, the Orinoco River basin is a mosaic of water types. Alfred Russel Wallace ([1853] 1972) was one of the first to mention the striking differences in water colors among the various South American waters using the terms whitewater, blackwater, and clearwater rivers. In a later and more detailed analysis, Sioli (1975, 1984) summarized differences among these three water types based on differences in water color, amount of suspended matter, and chemical properties. Whitewater streams are turbid because of inorganic sediments, of milk-coffee color (*cafe con leche*), relatively rich in nutrients, and of near neutral pH. Blackwater streams are transparent but reddish brown, the color of tea due to humic acids (the color appears black where water runs deep), very poor in nutrients and very acidic. Clearwater streams are also transparent, often greenish in color, typically poor in nutrients, and have a pH that can range from slightly acidic to slightly alkaline.

In the Orinoco River basin, whitewater and blackwater habitats predominate. Clear waters are more typical of small caños and the upland reaches of certain rivers. However, the classification of rivers by water color is not always easy to apply and thus the usefulness Sioli's classification scheme is somewhat limited. Many rivers are a mixture of

two or more of the basic water types; some change seasonally as flows from a diverse array of smaller tributaries rise and fall. For example, during high water the Guayapo River of the Sipapo drainage changes from a clearwater river in its upper and middle reaches to a blackwater river in its lower segments, due to increased input of tannin-stained waters from adjacent flooded forests. To a large extent, the hydrochemistry of the Orinoco tributaries is controlled by the geomorphological and floristic character of their watersheds. In general, rivers of the Andes and Llanos are high in suspended sediments, whereas streams originating in the weathered Guayana highlands and the forests of the upper Orinoco transport low sediment loads. Nevertheless, exceptions to the above-mentioned hydrochemical pattern can be found in all regions as a result of local conditions.

History of the Basin

The details and precise timing of geological events involved in the formation of the Orinoco River basin are not well understood. The oldest land form in the basin is the Guyana Shield, ancient mountains composed of Precambrian material that underwent additional uplift and exposure during the Tertiary (Whitmore and Prance 1987). Because they have been exposed for many millions of years, these highlands have been heavily worn and dramatically shaped by erosion. The mountains of the Andes were created later, uplifted as a result of plate tectonic events during the Miocene-Pliocene, 2-8 million years ago (Whitmore and Prance 1987:7). The Llanos are thought to be the most recent major topographical feature in the basin. During Quaternary periods of raised sea-level (interglacials) the Llanos plains were the bed of a large interior sea. Thus, similar to many lowland areas in South America, these central plains are primarily composed of Quaternary sediments that mantle Tertiary and older sediments, with recent additions of alluvial river deposits carried down from the surrounding mountains during the Pleistocene (Beek and Bramão 1968:86, Walter 1973: 72-73, Cole 1986).

An ancient Orinoco River is thought to have flowed to the northwest, emptying into the Caribbean before the Miocene uplift of the Andes near or through the present day Maracaibo Lake Basin. In addition to geologic evidence, this idea of a northward flow has received added support from comparisons of fossil and living fishes found in northern Colombia and Venezuela (Lundberg et al. 1986, 1988). According to the proposed scenario, the river slowly shifted to the east some time between the Late Cretaceous and early Oligocene, finally assuming its present course by the Oligocene epoch, about 30 million years ago (Lundberg et al. 1988). However, it is still uncertain how the river's movements affected or coincided with the formation and eventual draining of the sea that covered the interior lowlands at about the same time periods (Taphorn 1990).

The Orinoco and Amazon rivers are connected today by the Casiquiare canal, a natural waterway flowing southward from the upper Orinoco into the upper Rio Negro, permitting interchange of fishes between the two basins. However, the Orinoco and Amazon basins may have had an even closer association in the past, partly based on studies in western Brazil. The Amazon once flowed westward to the Pacific before the major rise of the Andes in the Miocene (Goulding 1980, Putzer 1984). After the Andes uplift blocked its westward flow, a huge lake, or more likely, a series of large lakes and wetlands, were formed covering much of the lowland areas in the basin (Frailey et al. 1988). Eastward flow was prevented at the time by higher elevations joining the Brazilian and Guyana shields. Before the Amazon had completely carved its way east between the two shields, the proposed Pleistocene/Holocene lake or lakes had their prime outlet north into the Orinoco. Indeed, tectonic events may have resulted in shifting the primary outlet several times between the north and east (Frailey et al. 1988).

The Low Llanos

The Llanos (Fig. 2-2) are a vast plain of up to 400 km width along the north bank of the Orinoco, stretching from near the delta mouth westward for over 1,000 km through Venezuela, far into Colombia (Walter 1973). It occupies about 500,000 km^2, is essentially unbroken by major forests, and is the largest continuous savanna in the neotropics north of the equator (Sarmiento 1984). A combination of factors, for instance soil type and rainfall patterns, prevent the establishment of forest in large parts of the Llanos. Dry season fires, of mostly human origin, are also important in limiting the growth of woody vegetation.

Several systems have been used to divide the Llanos into different categories using combinations of physical and biological features. In most cases, a distinction is made between the low Llanos and high or upper Llanos, based on elevation and extent of flooding during the rainy season (Walter 1973: 73, Cole 1986). The low Llanos are characterized by open grass savannas with fairly level terrain that undergo frequent or long term flooding during the rainy season. According to Cole (1986:92), savanna grasslands cover some 150,000 km^2 of the low Llanos in the Orinoco basin. Apure State, in western Venezuela, encompasses a large portion of the low Llanos. Here the terrain is relatively flat, with elevations of 100 m or less above sea level. In Apure, the landscape is dominated by herbaceous cover, mainly bunch grasses and sedges, with occasional shrubs and small trees (Sarmiento 1984, Cole 1986). Most trees, including palms, exist in small isolated groups (*matas*) or in gallery forest situations fringing the rivers and larger streams (Sarmiento 1984, Cole 1986). These gallery forests range from narrow bands, only a few trees wide, to fairly extensive stands, in some places many hundreds of meters wide, as seen existing along reaches of the lower Cinaruco and Capanaparo rivers.

The low Llanos of Apure State (Fig. 2-3) comprise a vast open floodplain containing a diversity of aquatic habitats (Mago-Leccia 1970). All undergo pronounced seasonal changes. Because of its low elevation and flat physical relief, most of the

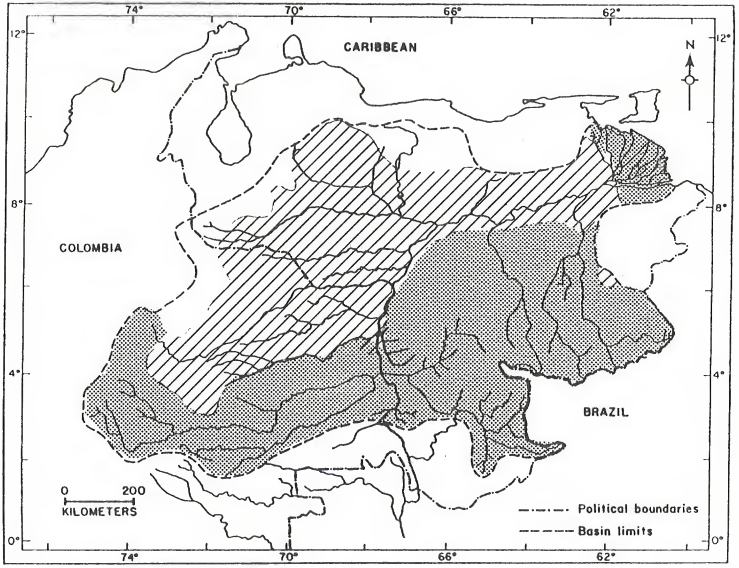


Fig. 2-2. Major savanna (hatched) and forest (shaded) ecosystems in the Orinoco River basin.

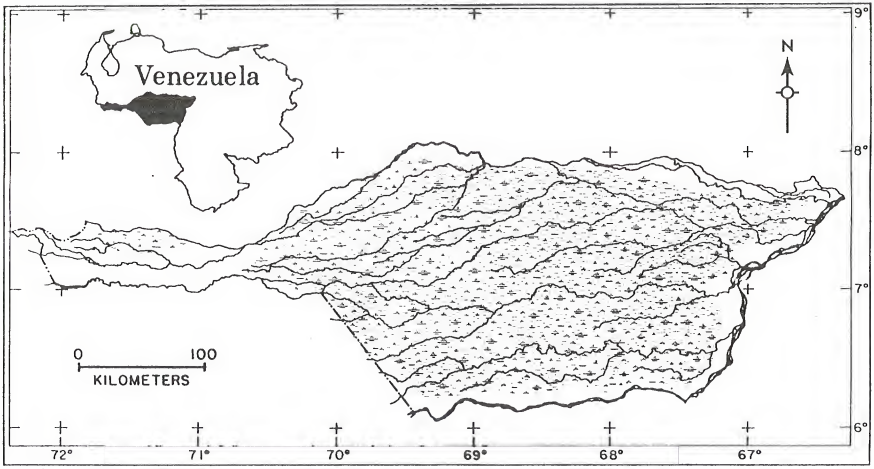


Fig. 2-3. Approximate distribution of open savanna (low Llanos) in Venezuelan state of Apure, Orinoco River basin.

landscape floods during the rainy season, whereas surface water during the dry season is usually limited to a few large permanent lagoons, large streams, and rivers. As the dry season progresses, the savanna vegetation turns yellow and the earth becomes hard and is fissured with cracks from the intense heat of the sun. Rivers and streams in the low Llanos are of low gradient, with many wide meanders and anastomoses. The Apure River and many of its tributaries are whitewater in character, with a relatively high sediment load and high conductance (Saunders and Lewis 1988). In contrast, the Capanaparo and Cinaruco are essentially blackwater rivers, with moderate sediment loads. In addition to stream channels, the landscape of the low Llanos is dotted with shallow marshes (*esteros*) that hold water after floods or rain. Lagoons (*lagunas*) form in deeper depressions, some created from abandoned stream meanders, and are more permanent aquatic habitats. Human population density is low and most of the low Llanos is used for cattle ranching. Since the early 1970's extensive networks of low earthen dikes, called modules (*módulos*), have been constructed, surrounding large areas of the floodplain savanna. These modules lessen the extreme effects of seasonal changes within their boundaries by controlling flooding and by holding water in lower areas, available to cattle year round. The hundreds of borrow pits (*prestamos*) excavated during the construction of these dikes, as well as from building of roads, collect water and serve as permanent and semi-permanent artificial lagoons. Typically less than 25 m wide, some prestamos stretch unbroken for several kilometers.

During high water, adjacent rivers and streams in the Llanos are often connected by sheet flooding of the savanna or by filling of small interconnecting channels. Thus, fish are generally able to move across the entire floodplain. However, where dikes or roadways are present, run-off patterns have changed and local fish movements are somewhat restricted (Taphorn and Lilyestrom 1984, Nico and Taphorn 1988).

Many of the wetlands in the Llanos contain large amounts of organic material and become highly productive during the rainy season (Mago-Leccia 1970, Saunders and

Lewis 1988). During high water, the flooded savanna habitats are important to fish as breeding and feeding areas. Aquatic vegetation flourishes and emergent and floating plants may cover large portions of the surface of both permanent and temporary water bodies. Large mats of water hyacinth (*Eichhornia* species) are especially abundant in many of the lagoons, prestamos, and some of the streams. Partially inundated grasses and sedges commonly grow in the shallows of streams, prestamos, and other standing waters. Other common aquatic and semi-aquatic plants of the low Llanos include *Ludwigia*, *Benjamania*, and *Pontederia*. Some common aquatic plants with floating leaves are *Salvinia*, *Lemna*, and *Pistia*.

The Upper Orinoco

The upper Orinoco drainage is situated in the Federal Territory of Amazonas (Fig. 2-4) in southern Venezuela, a vast area covering 178,095 km^2 (CODESUR 1979). Main features of the heavily forested landscape are flat alluvial plains, large mountain valleys, and massive granitic hills (*lajas*) (CODESUR 1979, Huber and Wurdack 1984). About 70 percent of the territory is drained by the Orinoco, with the remainder flowing into the Rio Negro of the Amazon basin (CODESUR 1979). Together with the adjacent state of Bolivar, this southern section of the country is often referred to collectively as Venezuelan Guyana because the Precambrian Shield dominates the topography. Little developed and with few inhabitants, the great majority of intact forests in Venezuela occur in this southern region. Steyermark (1982) estimated that forests covered 82 percent of the region, or about 146,000 km^2. Due to forest clearing, the total coverage is probably slightly less today. Because forests of the upper Orinoco are continuous with those of the northern Amazon Basin, the region is part of the largest area of humid forests within the neotropics (Whitmore and Prance 1987).

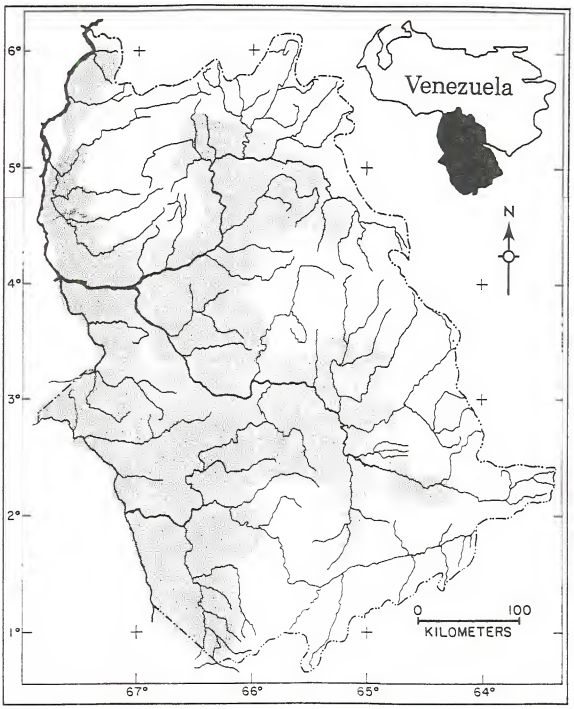


Fig. 2-4. Approximate distribution of lowland forests (shaded area) in Federal Amazon Territory of Venezuela.

The flat lowlands or peneplains of southern Venezuela are dominated by wet tropical forests (Figs. 2-2 and 2-4). The altitude of these lowland regions in the upper Orinoco range from 100 to 500 m, with most less than 200 m (Huber and Wurdack 1984). Similar to the situation described for Amazonian lowlands (Prance 1979, Kubitski 1989), many lowland forests in the upper Orinoco are inundated by the annual high water, with some sites being permanently waterlogged. Aerial photos of the lowlands reveal a history of streams meandering across their adjacent floodplains. Large and small streams, cutoffs, and oxbows abound in many of the drainages (e.g., Mavaca River) and, similar to the low Llanos, interconnections with adjacent drainages within the upper Orinoco are common during high water. However, aquatic vegetation in the region is much more sparse and localized in comparison to the low Llanos. Although a few backwaters are choked with submergent and emergent vegetation, most floodplain lakes in the upper Orinoco have few or no aquatic plants. The reasons for such scarcity are likely related to high shade, unconsolidated bottoms, and few available nutrients in the water or substrate. In flowing waters there are often small bands of flooded grasses along bank edges of inner bends. The fish fauna of the upper Orinoco is the least known in all of Venezuela, largely because of the inaccessibility of the region. With very few roads, modes of transportation within the area are limited almost exclusively to small and medium-sized boats and small planes.

Savannas and Forests during the Quaternary

Both tropical forest and tropical non-forest vegetation originated in the Cretaceous and Tertiary, about 100 million years ago, periods when world climates were apparently rather stable and tropical conditions much more widespread (Whitmore and Prance 1987). However, during the last two million years there have been periodic and dramatic fluctuations in the distribution of savannas versus forest environments in northern South

America that are associated with climatic oscillations (Prance 1982, Whitmore and Prance 1987). Although lowland regions remained essentially tropical, during major glaciations the equatorial lowland regions experienced dryer and hotter climates (but see Colinvaux 1976). As a result, savanna and open-land environments expanded, whereas humid forests contracted. During these dry periods, forests were often reduced to combinations of variably-sized isolated refuges and fingers of gallery forests along major rivers. Indeed, new data on Pleistocene mammals indicate that savanna habitat may have expanded to such an extent as to form a continuous band connecting the Orinoco Llanos with the pampas of Argentina by way of the western Amazon basin (Rancy 1991). The last major glacial event causing a cold, dry Pleistocene climatic phase occurred 13,000-18,000 years ago.

Much controversy exists about the extent and precise location of forests during the Pleistocene dry periods. Haffer (1987:12) presented a map outlining possible distribution of both relatively humid areas and tropical forests, forest "refugia", surviving in northern South America during that period of savanna expansion. His map delineates three major regions of humid forests in the Orinoco basin: several sections in the Andes; a block near the southern tip of Venezuela; and a long broad belt (100-200 km wide) south of the main stem Orinoco, extending from near the mouth of the Meta River eastward through the Guianas.

In contrast to glacial periods, interglacial or pluvial periods were wetter and relatively cooler, contributing to the expansion of humid forests and contraction of savannas. Isolated savannas currently found in the upper Orinoco are thought to be savanna refugia that survived the cooler and wetter phases. The present climatic condition is wet and warm (i.e., as opposed to dry and hot), and humid forests are at or near their maximum extent, whereas the extent of natural savannas and dry forests is restricted (Whitmore and Prance 1987:63).

Present Climate and Seasonality

Regional topography and the fact that the entire Orinoco Basin lies immediately north of the equator are important factors controlling climate and the timing of precipitation (Walter et al. 1975). There is a trend toward increased rainfall from north to south. Nevertheless, rainfall patterns can be quite variable from year to year in a single locality, as well as among different localities within any particular region.

The Llanos have consistently high temperatures and fairly distinct wet and dry periods. The rainy season is associated with the inner-tropical convergence zone (Walter et al. 1975), and lasts from seven to nine months, usually from late April to October or November (Fig. 2-5). Little or no rain falls during the two or three driest months, when the inner-tropical convergence zone is in the southern hemisphere. Total rainfall in the Llanos ranges from 1200 to 1800 mm per year (Taphorn 1990), with savanna grasslands common to the low Llanos typically receiving 1300-1400 mm (Cole 1986:97). The recording station at San Fernando de Apure, located in the center of the low Llanos, reported a mean annual precipitation of 1416 mm, based on 26 years of records (Walter et al. 1975); mean monthly temperatures for the locality varied between 26.6 and 29.2 °C (Cole 1986:97). However, daily temperatures can fluctuate widely.

Although the two regions have a fairly similar range of air temperatures, the upper Orinoco is much more humid than the Llanos. Average annual rainfall is 3,250 mm/yr, with very humid areas receiving well over 4,000 mm (CODESUR 1979). Although the amount of rainfall varies seasonally, the dry season in the upper Orinoco is not as pronounced as in the Llanos (Fig. 2-5). Few areas of record receive less than 75 mm in any given month during the dry season (CODESUR 1979). Nevertheless, the alternation of low and high water seasons is distinct. Highest precipitation occurs between May and September and the lowest between December and March (CODESUR 1979). Monthly mean temperatures range from 26 to 28.5 °C (CODESUR 1979). Both the low Llanos of

Apure State and the lowland forests of the upper Orinoco undergo extensive flooding during the wetter part of the year by a combination of rising river water and local rains.

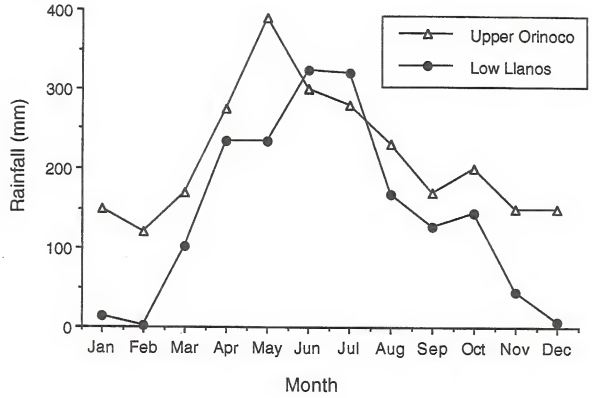


Fig. 2-5. Monthly rainfall recorded at representative sites in Orinoco River basin, Venezuela. (1) Upper Orinoco: monthly average 1971-1977 from Santa Maria de Los Guaicas, mouth of Ocamo River, Federal Territory of Amazonas, and (2) Low Llanos: for year 1972 from Caño Caicara area, Apure River drainage, Apure State. Sources: CODESUR (1979) and Taphorn and Lilyestrom (1984), respectively.

CHAPTER 3
METHODS

Field Sampling

In the field I tried to collect as many individuals, sizes, and species of serrasalmine fishes as possible from each region and drainage, but I did not attempt to measure fish biomass. Sampling of fishes was done in all major habitats using appropriate combinations of collecting gear and fishing tactics so as to obtain the most information in a short period of time. Although piranhas were taken in greatest numbers during the day, especially near twilight, night collections were also made in the two major regions studied. For sampling piranhas, I depended mainly on various combinations of seines, gill nets, cast nets, and hook and line. Harpoons, spear gun, minnow traps, trotlines, and commercial (5% rotenone) and natural (*barbasco*) fish toxicants were used only rarely; these capture methods contributed little to the total sample of serrasalmine fishes taken. In the field, most fishes collected were preserved immediately in 10-20% formalin; in the laboratory, preserved specimens (those less than about 200 mm SL) were transfered to 70% ethanol or 35% isopropanol. A few young piranhas were kept alive and maintained in aquaria.

Each type of sampling gear targeted a certain size range of fishes. For collecting young piranhas and other small fishes, I used small nylon seines (6x2 and 5x2 m, 6.4 mm mesh), nylon and monofilament cast nets ranging from 1.8 to 3 m diameter (2 to 2.5 cm mesh), and hand nets (3 mm mesh); these were normally limited to use in shallow areas (<1.5 m deep). Small seines and hand nets were the most effective equipment for sampling in areas with dense aquatic vegetation. In instances where vegetation made it difficult to

effectively pull the seine forward, a seine was set stationary, and one or more "kickers" drove fishes from the vegetation into the net.

Nylon bag seines (6x2 m with 2x2 m bag, 6.4 mm mesh) or large beach seines (10x2 m, 6.4 mm mesh) were used in more open shallow water habitats. These nets sampled for a broad range of fish sizes, but because few areas had clean substrates, large seines were usually limited to open beaches along rivers or streams, and lagoons, where there was little submerged debris.

Nylon and monofilament gill nets with float lines were used to sample selectively for medium and large-sized fishes, including adult and subadult piranhas. Gill net sizes were 20x2 m (20 cm stretch mesh), 10x5 m (5 cm mesh), 50x2 m (with two 25-m long panels of 5 and 7 cm mesh, respectively), and 100x2 m (6 cm mesh). For taking piranhas, gill nets were set in areas with little or no current, used in conjunction with seines, and in deeper water (>1.5 m) where use of seines was impractical. Set gill nets were monitored and all fish removed every 0.5 to 6 hours, depending on time of day and local fish abundance. Because piranhas can damage gill nets, nets set in areas with high piranha densities were checked more frequently.

All piranha species occurring in the Orinoco River basin take baited hooks (personal observation). Hook-and-line fishing was done mostly with natural bait, using hand lines and occasionally rod and reel. Different sizes and types of commercial hooks were used to sample for fishes of different sizes. Type of bait employed was noted so as to not be mistakenly recorded later as part of their natural diet. In general, sampling by hook and line yielded the same piranha species, and proportions of individuals, as those caught by gill net.

Overall, piranha species that were common in any one area were taken by two or more types of sampling gear. No one capture technique seemed to be selective for a particular piranha species, or group of species. Seines, gill nets, cast nets, and hook and

line were all occasionally effective in capturing species considered uncommon in a particular drainage or region.

To reduce the risk of missing uncommon or rare species in upper Orinoco drainages, where most sampling was limited to relatively short periods, I supplemented my own samples with collections of others. In the field, I recorded the catch of hired fishermen and Indians, including the daily hook-and-line collections of camp workers.

Field Site Locations and Sampling Periods

Nine drainages of the Orinoco River basin in Venezuela were sampled during the present study, three in the low Llanos and six in the upper Orinoco (Fig. 3-1).

Low Llanos or Savanna Sites

Three major drainages were studied in the low Llanos of Apure State: the Apure, Cinaruco, and Capanaparo rivers (Fig. 3-2). Principal habitats sampled were rivers, streams, natural and artificial lagoons and pools, and flooded savanna. The Apure drainage was the only site where long-term research on piranhas was carried out.

Apure Drainage. Almost all fieldwork was done in the Caño Caicara watershed of the Apure drainage in and around the Fernando Corrales research station and ranch of the Universidad de Los Llanos (UNELLEZ) (07°25'50"N, 69°35'30"W). This area is bordered by Caño Caicara, its tributary Caño Maporal, and a smaller stream, Caño Guaritico. I made periodic samples in the Caño Caicara study area during December 1983; January, March, May, July, September, and November 1984; and March, April, and May 1985; these were followed by samples taken during August 1988, March, April, and December 1989, and January, March, and May 1990. I also examined material taken

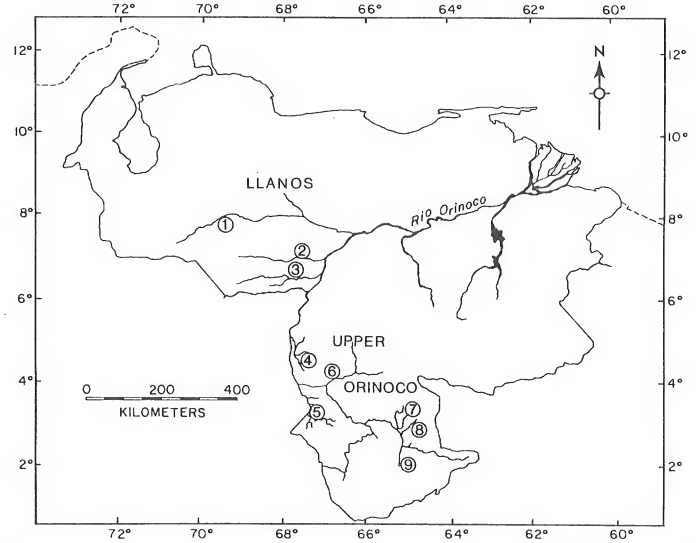


Fig. 3-1. Map of Venezuela showing nine selected drainages in Orinoco River basin sampled during present study. Low Llanos rivers: (1) Apure, (2) Capanaparo, and (3) Cinaruco; Upper Orinoco rivers: (4) Sipapo, (5) Atabapo, (6) lower Ventuari, (7) Matacuni, (8) Ocamo, and (9) Mavaca.

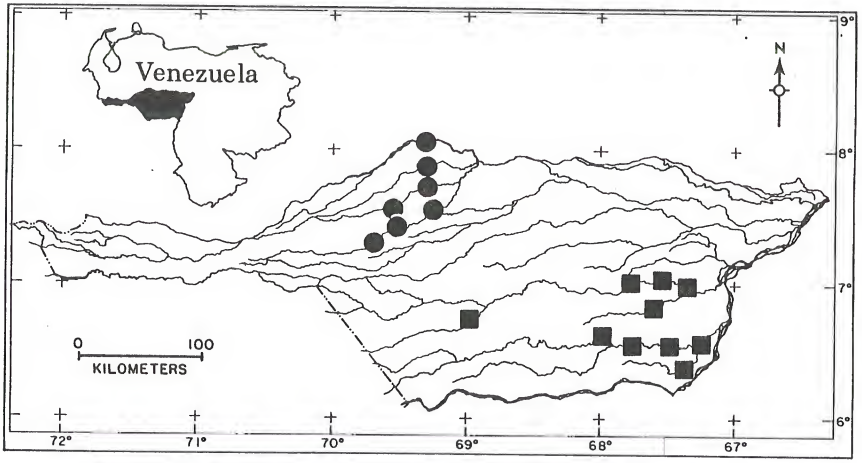


Fig. 3-2. Map of Apure State, Venezuela, showing principal low Llanos sampling sites. Solid circles represent localities sampled by the author; solid squares represent areas collected by others (specimens from all sites deposited at MCNG and examined by the author). Each symbol may represent more than one sampling site.

between 1979 and 1984, which included monthly samples of a one-year biomass study of the area in 1982-1983 (see Taphorn and Lilyestrom 1984). A total of about two hundred fish collections were made in the Apure River drainage in caños Caicara and Maporal and their adjacent floodplains from 1979 to 1990.

Cinaruco and Capanaparo drainages. I examined collections made by others from the lower Cinaruco and Capanaparo rivers and their floodplains. Most sites sampled were within 50 km of the north-to-south road joining San Fernando de Apure with Puerto Paez, a route roughly following 67°30' W longitude. Samples were taken in January 1982, December 1986, January 1987, and March and April 1989. The 1989 collections were the result of a fish inventory of the two drainages made by D. C. Taphorn and A. Barbarino using seines, cast nets, and hook and line. Overall, sites collected were the main channels and near-shore areas of the two rivers, as well as Laguna Larga of the Cinaruco River, and Caño La Pica and Laguna Brava of the Capanaparo drainage.

Upper Orinoco or Forest Sites

Six major drainages in the upper Orinoco, Amazon Territory of Venezuela, were sampled for analysis of piranha populations from forested regions (Fig. 3-3). These included the Sipapo, Atabapo, Ventuari, Matacuni, Ocamo, and Mavaca drainages, as well as the main channel of the Orinoco River. I collected fishes and evaluated habitats during five expeditions, between early 1989 and 1991, as part of a resource inventory of southern Venezuela in association with the mineral consortium CVG-TECMIN (Corporación Venezolana Guyana - Tecnica Minera). Data on serrasalmine fishes from the region are based on intensive sampling of many sites over relatively short periods of time. Each expedition lasted between 25 and 40 field days and covered a different drainage or set of

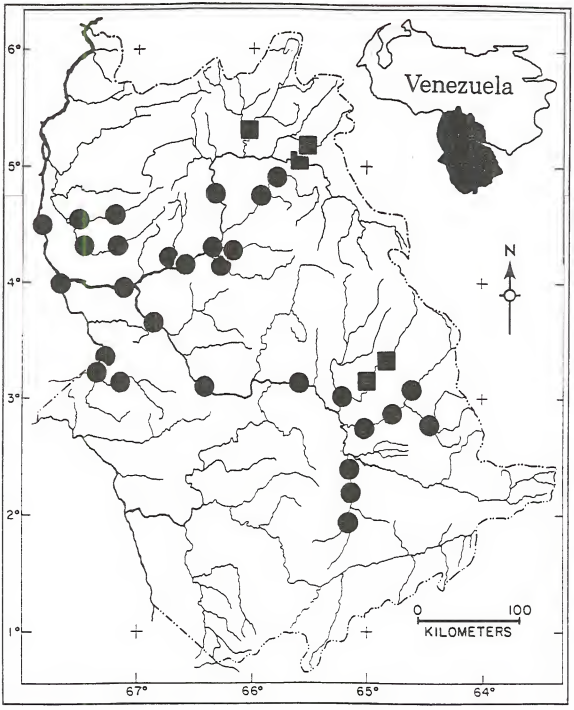


Fig. 3-3. Map of 1988-1991 sampling sites in upper Orinoco, Federal Territory of Amazonas, Venezuela Solid circles represent localities sampled by the author; solid squares represent areas collected by others (specimens from all sites deposited at MCNG and examined by the author). Circles and squares may represent more than one sampling site.

drainages. Work in any one drainage was usually limited to one part of the year, either during the high or low water period.

Lowland habitats sampled in the upper Orinoco were channel borders and beaches of rivers, streams, side channels, old meanders and other back waters, including isolated floodplain lakes, as well as inundated forest. Elevations ranged from 90 to about 240 m above sea level. Collection sites and sampling dates were as follows: (1) Guayapo and Sipapo rivers, from 12 May to 7 June, 1989; (2) lower Ventuari River, including its tributaries the Yureba, Parú, Asisa, Guapuchí (= Picure), Marueta rivers and the caños Cucuritál, Moriche and Tabi-Tabi, from 17 September to 16 October, 1989; (3) Atabapo River, including its tributaries the Atacavi and Temi rivers and the caños Patacame, Cuchakén, Bocachico, and Chimita, from 23 October to 17 November, 1989; (4) Ocamo, Putaco, Padamo, and Matacuni rivers, and the caños Jayuwapuei, Jenita, Maveti, and Yaraca-bawei, including the upper Orinoco River main channel above its confluence with the Ventuari, from 16 January to 16 February, 1990; and (5) Mavaca River, its tributary Caño Mavaquita (= Caño Hauyapiwei), and the upper Orinoco main channel, from 18 January to 20 February, 1991. A total of 200 fish collections representing 180 individual sites was made in this region, resulting in over 18,000 specimens, of which 500 were serrasalmine fishes.

Evaluation of Habitats

A variety of habitat parameters was recorded whenever possible for most collection sites. Qualitative and quantitative estimates were as follows: (1) season (wet, dry, or transitional); (2) water type (clear, black, white, or combination); (3) water level (isolated pools, continuous in bank, bank full, or flood condition); (4) watershed topography (level, moderately rolling, rolling, mountains); (5) stream gradient (flat, slight, moderate, or >30 degrees); (6) land use (natural, cattle, agricultural, or developed); (7) major terrestrial

habitat (grassland, savanna, gallery forest, or forest); (8) dominant riparian vegetation (none, grasses/forbes, shrubs/trees, narrow forest border, or forest); (9) water depths at site and capture depths (very shallow [0-5 cm], shallow [5-20 cm], moderate [20-50 cm], deep [50-100 cm], very deep [100-150 cm], extremely deep [>150 cm]); (10) water velocities, as measured with a mechanical flowmeter (General Oceanics) or using a floating stick or cork, were classified into six categories (zero [<0.02 m/sec], very slow [0.02-0.10 m/sec], slow [0.10-0.25 m/sec], moderate [0.25-0.75 m/sec], fast [0.75-1.25 m/sec], and torrential [>1.25 m/sec]); (11) water temperature; (12) water pH measured with a Hach pH Pocket Pal meter or a Hach colorimetric (color disc) wide range pH test kit (Model 17-N); (13) water color and turbidity (very-clear, clear-tannin, clear-green, slightly-turbid, moderately turbid, or very turbid); (14) water clarity as measured with a 20-cm diameter Secchi disk; (15) estimated maximum and average water width; (16) degree of shading (full sun, partial shade, temporary full shade, permanent full shade).

Substrate types and types of aquatic or instream cover for each collecting site were recorded by estimating their proportion of the total surface area: (0)=none/few; (1)<10%; (2)10-50%; and (3)>50%. Substrate types recognized were: silt/mud; sand; gravel; rubble; boulder; bedrock/claypan; vegetation; litter; and detritus/decomposed organics. Fish cover categories recognized were: floating aquatic vegetation; emergent vegetation; submergent vegetation; litter on bottom; overhanging vegetation; undercuts; bank cover; brush/roots; rocks; logs; and artificial structures (e.g., culverts, bridge piers).

Identification and Nomenclature of Piranhas

At least 12 species of piranha occur in the Orinoco River basin (personal observation). As with most groups of South American freshwater fishes, there has been a great deal of confusion surrounding the classification and nomenclature of the subfamily Serrasalminae, due to a combination of factors. Some species exhibit marked changes in

body shape with growth. Individuals are also fairly variable in terms of body pigmentation and color patterns; such differences can be associated with age, size, or sexual condition, and may also be environmentally induced. To further complicate piranha taxonomy, the complete geographic distribution of most species is unknown. Moreover, because little if any comparative material was available to previous taxonomists, most earlier descriptions were incomplete, and thus inadequate for making accurate identifications. Fink (1988) reported that fewer than half of the about 60 nominal species of piranhas were valid. Nevertheless, sampling in previously uncollected regions has resulted in the discovery of a few new species (personal observation). Except for difficulties in identifying some of the smallest specimens (less than 25 mm SL), I believe I have successfully sorted out the different species encountered in this study. Preserved specimens examined are deposited in the Museo de Ciencias Naturales (MCNG), UNELLEZ, Guanare, Venezuela. Voucher material has also been donated by MCNG under an official cooperative agreement to the Florida Museum of Natural History (UF), Gainesville, Florida. Institutional acronyms are from Leviton et al. (1985).

Because of the taxonomic confusion, piranhas have often been misidentified in the literature. Drs. William Fink (UMMZ) and Antonio Machado-Allison (MBUCV) are currently revising the piranhas of Venezuela; I have relied on both for identifications of certain voucher specimens. They have also made available their unpublished key to Venezuelan piranhas. Taphorn (1990) prepared keys to the characiform fishes of the Apure drainage, and also listed probable generic and specific synonyms of serrasalmine fishes. His nomenclature for piranhas follows that of Fink and Machado-Allison. Abbreviations used for piranhas and other serrasalmine fishes in illustrations and tables are given in Table 3-1. In the following section species names used in the present report are listed together with names used by me and colleagues for the same species in recent publications:

(1) *Serrasalmus altuvei* Ramírez 1965: *Serrasalmus altuvei* in Nico and Taphorn (1988); color illustrations in Nico and Taphorn (1986:33), photos reproduced in Schulte (1988:119).

(2) *Serrasalmus* cf. *eigenmanni* Norman 1928: *Serrasalmus* cf *eigenmanni* may involve a species complex (W. Fink, personal communication): however, I distinguished only one species in my samples. This species, to my knowledge, has not been previously referenced in publications on Venezuelan piranhas. The piranha *Serrasalmus nalseni* described and figured by Fernández-Yépez (1969) is a possible synonym, but I have not seen the type series. All previous references to *Serrasalmus eigenmanni* from the Orinoco probably refer to other species (see *Serrasalmus irritans* below).

(3) *Serrasalmus elongatus* Kner 1860: *Serrasalmus* cf. *elongatus* in Taphorn and Lilyestrom (1984), Nico and Taphorn (1988); color illustrations in Nico and Taphorn (1986), photos reproduced in Schulte (1988:1, 119); photos as *S. pingke* in Román (1983:56).

(4) *Serrasalmus irritans* Peters 1877: *S. eigenmanni* in Taphorn and Lilyestrom (1983); *S. irritans* in Nico and Taphorn (1988) and Winemiller (1989a, 1989b); color illustrations as *Serrasalmus eigenmanni* in Nico and Taphorn (1986:31, 33), same photos reproduced in Schulte (1988:120), photos as *S. eigenmanni* in Román (1983:57).

(5) *Serrasalmus manueli* Fernández-Yépez and Ramírez 1967: This species has rarely been referenced in the literature since its original description. I am unaware of misidentifications. There is no published information on its biology or natural history.

(6) *Serrasalmus medinai* Ramírez 1965: *Serrasalmus caribe* in Nico and Taphorn (1988); incorrectly spelled as *S. medini* in Winemiller (1989a, 1989b); color illustrations as *Pristobrycon* sp. in Nico and Taphorn (1986:31, 33, 41), photos reproduced as *Serrasalmus* (*Pristobrycon*) sp. in Schulte (1988:119), and as *Serrasalmus* (*Pristobrycon*) "iridescent" (incorrect locality given) in Schulte (1988:128); photos as *S. rhombeus* in Román (1983:31,60).

Table 3-1. List of abbreviations used in figures and tables for piranhas and other serrasalmine fishes.

Piranhas:		Other Serrasalmine Fishes:	
Pc	*Pygocentrus caribe*	Cm	*Catoprion mento*
Psp	*Pristobrycon* sp.	Mag	*Metynnis argenteus*
Pst	*Pristobrycon striolatus*	Mya	*Myleus asterias*
Pyp	*Pygopristis denticulatus*	Mys	*Myleus schomburgkii*
Sa	*Serrasalmus altuvei*	Myt	*Myleus torquatus*
Seg	*Serrasalmus* cf. *eigenmanni*	Md	*Mylossoma duriventris*
Sel	*Serrasalmus elongatus*		
Sir	*Serrasalmus irritans*		
Sm	*Serrasalmus manueli*		
Smd	*Serrasalmus medinai*		
Sr	*Serrasalmus rhombeus*		

(7) *Serrasalmus rhombeus* (Linnaeus) 1766: *Serrasalmus rhombeus* in Nico and Taphorn (1988) and Winemiller (1989a, 1989b); and color illustration in Nico and Taphorn (1986:40-41).

(8) *Pygocentrus caribe* Valenciennes 1849: *Pygocentrus notatus* in Taphorn and Lilyestrom (1984), Nico and Taphorn (1988), Winemiller (1989a, 1989b), Nico (1990); color illustrations are given as *P. notatus* in Nico and Taphorn (1986:31, 40, 41), photos reproduced as *Serrasalmus* (*Pygocentrus*) *notatus* in Schulte (1988:109, 110), as *Serrasalmus niger* in Schulte (1988: 111), and as *Serrasalmus nattereri* (incorrect locality given) in Schulte (1988:12-13).

(9) *Pristobrycon striolatus* (Steindachner) 1908: *Pristobrycon striolatus* in Nico and Taphorn (1988); color illustrations as *Pristobrycon striatus* in Nico and Taphorn (1986:31, 41), and as *Pygocentrus striolatus* in Nico and Taphorn (1986:33), photo reproduced in Schulte (1988:120). Machado-Allison et al. (1989) concluded that *Pygopristis antoni* Fernández-Yépez, 1965 is a junior synonym of *P. striolatus*.

(10) *Pristobrycon* sp.: This species is in the process of being described as new by W. Fink and A. Machado-Allison.

(11) *Pygopristis denticulatus* Muller and Troschel 1844: photograph as *Serrasalmus* (*Pygopristis*) *antoni* in Román (1983:51).

Faunal Comparisons

The Coefficient of Biogeographic Resemblance (CBR) proposed by Duellman (1990) was used to compare the composition of piranha assemblages between the two regions studied and among the different drainages. This qualitative index of similarity has been reinvented a number of times, consequently it is known by several names including the Faunal Resemblance Factor, the Sorenson Index, and the Dice Coefficient (Boesch 1977, Romesburg 1984, Magurran 1988, Duellman 1990). This index is one of the more

commonly used measures for comparing species presence-absence data (Krebs 1989), and is calculated as:

$$CBR = 2C/ (N_1 + N_2),$$

where C is the number of species common to two areas, N_1 is the number of species in the first area, and N_2 is the number of species in the second area. The resulting values range from 0, if there are no species in common, to 1, if both areas share the same number and kinds of species. This measure is simple, is not affected by relative numbers of individuals, and thus is best used when there are no reliable quantitative data on abundance of species (Magurran 1988, Krebs 1989). Binary similarity measures are not totally independent of sample size (Wolda 1981, Krebs 1989). However, comparisons when maximum number of possible species is low give results less affected by sample size differences than those dealing with many species (see Krebs 1989). CBR is very similar to the Jaccard Coefficient (Boesch 1977, Romesburg 1984, Duellman 1990); it doubly weights shared positive attributes (i.e., joint presences), and is preferred over the Jaccard Coefficient if the entities vary widely in their number of positive attributes (Boesch 1977:22).

To make presence-absence data more reliable, I supplemented my data with information from collections deposited at MCNG and UF. I also reviewed the literature for records of species occurrence. A Spearman rank correlation test was used to test for an association between species composition and drainage area size, and between faunal similarities and distances among drainages. The similarity or resemblance matrix generated from the CBR equation was used as a basis for clustering drainages, employing the unweighted pair-group method using mathematical averages, or UPGMA.

Analysis of Diets

In order to analyze diets and document ontogenetic shifts in feeding, sampled fishes were divided into five size classes: Group I) 10-19 mm SL - small juveniles; Group II) 20-39 mm SL; Group III) 40-79 mm SL; Group IV) 80-159 mm SL; and Group V) ≥160 mm SL. Several species were not represented by all size classes.

During the study, more than 2,000 serrasalmine fishes were captured; total number of specimens examined for stomach contents was 1,538 from the low Llanos and 393 from the upper Orinoco. Standard length (SL) of each specimen was measured to the nearest mm. Although a few of the largest fish were dissected and examined in the field, most specimens were preserved after capture and dissected later in the laboratory to determine stomach contents. I examined stomach contents and recorded frequency of occurrence (O), number (N), and dominance by bulk (D) for each food item. I also recorded volume (V) of food items found in stomachs of fishes taken in the field after 1986. Small food organisms were counted using a Ward counting wheel under 25X magnification. Volume was determined by water displacement using appropriately-sized graduated cylinders. Volumes of smaller items were calculated by measuring dimensions with Vernier calipers or by examination under a dissecting microscope and comparison with known volumes. An estimate of relative stomach fullness was made using scores ranging from 0 (empty) to 3 (if full, or almost full) (Thomerson and Wooldridge 1970, Nico and Taphorn 1988).

For specimens collected in the Apure River drainage before 1986, I estimated volume using a point system, referred to as adjusted volume (V_a), and derived from D and stomach fullness (Nico and Taphorn 1988). That is, only the dominant food categories of a given stomach were included and each was assigned the fullness points (1-3) for that stomach. If two food items in a single stomach were of about equal volume, each received half the fullness value. Thus, $\%V_a$ = total fullness points for each food category as a percentage of all fullness points, and can be shown as:

$$\%V_a = \left(\sum_{n}^{i=1} F_i \,/\, \sum_{n}^{i=1} T_i \right) \times 100,$$

where F_i is the fullness points for stomachs whose dominant food item is F; T_i is total fullness points for all stomachs; and n is the number of stomachs examined of a species or size class.

I attempted to identify food items to the lowest taxonomic level, whenever possible. For comparing piranha diets, I recognized eleven general food categories: (1) masticated seeds - crushed or fragmented seeds together with the hard parts (mainly endocarp)that surround the seed; (2) other plant material - mostly leaves, root fragments, fleshy fruits, and flowers; (3) decapods - crabs and shrimp; (4) microcrustaceans - copepods, cladocerans, ostracods and conchostracans; (5) aquatic insects - various families, including larvae and adults; (6) other invertebrates - mostly arthropods, including terrestrial forms, but also aquatic nematodes and snails; (7) small whole fish - at least two-thirds of total body; (8) fish flesh - pieces of flesh bitten from fish; (9) fish fins - fins not taken with or attached to pieces of flesh; (10) fish scales - scales not taken with or attached to flesh; and (11) other - detritus, sand, nonfish vertebrates, and unidentifiable items.

I compared and contrasted diets within and among the different species and size groups by calculating estimates of diet breadth and overlap based on percent food volume or adjusted volume. Because I did not quantitatively measure the relative availability of food resources in the field, I chose two widely used indices of breadth and overlap that do not take into account the relative abundance of the various food items in the natural environment.

Diet breadth, or width, measures the diversity and evenness of resource use. Diet breadth was computed for each species' size class using Levins' index of niche width (Levins 1968, Krebs 1989):

$$\text{Diet breadth } (B) = 1/ \sum_{n}^{i=1} P_i^2,$$

where P_i is the proportion of food category i in the diet. B ranges from 1, when one resource state is used exclusively, to n (the total number of food categories recognized), when all resource states are used in equal proportion. This measure is the reciprocal of Simpson's index of diversity (Krebs 1989).

I used the Schoener Overlap Index (Schoener 1970) to estimate the similarity in diets between and within species. This particular index is also known as the Renkonen Index, the Percent or Proportional Similarity Index, Percentage Overlap, and Czekanowski's Index (Krebs 1989); the Bray-Curtis Coefficient gives the same results as the above index if its scores are standardized (Boesch 1977:26, Bloom 1981). The Schoener Overlap Index is calculated as:

$$\text{Overlap} = 1 - 0.5 \left(\sum_{n}^{i=1} | p_{xi} - p_{yi} | \right) = \sum_{n}^{i=1} (\text{minimum } p_{xi}, p_{yi}),$$

where p_{xi} is the proportion of food category i in the diet of species x, p_{yi} is the proportion of food category i in the diet of species y, and n is the number of food categories. The Schoener Index gives values from 0 to 1 (or 0 to 100%) indicating no overlap to complete similarity in the proportion of food categories used by the two groups compared.

There are many indices available for estimating niche or diet width and overlap, but as yet there is no general consensus as to which of the many indices is best (Hurlbert 1978, Abrams 1980, Wallace 1981). Recent reviews of frequently used indices include Ludwig and Reynolds (1988) and Krebs (1989). All measures of breadth and overlap are biased in some way, the bias usually being reduced with increasing sample size (Schluter 1988, Krebs 1989). It has also been shown that measures of breadth and overlap are sensitive to the number of resource categories used. Although lumping resource states can inflate niche

overlap values (Greene and Jaksíc 1983), bias increases as the number of resource categories used increases or is large (Ricklefs and Lau 1980, Smith and Zaret 1982, Krebs 1989). Overlap and breadth indices also give somewhat different results depending on the methods used to tabulate dietary components, for example, percentages based on total food volume, weight, frequency of occurrence, or food item number (Wallace 1981). An additional problem implicit in all overlap and breadth measurements is that the investigator may recognize resource categories that animals do not. For instance, Goulding et al. (1988:52) suggested that Amazonian frugivorous fishes "select their preferred fruits and seeds at what taxonomically are referred to as genera" rather than at the species level. Conversely, organisms may distinguish resources lumped together by human observers (Ludwig and Reynolds 1988, Krebs 1989). Finally, most overlap and width indices are based on the relative use of different resources, without accounting for their relative availabilities. However, resource availability is difficult to assess and therefore rarely measured. Those indices that do incorporate some estimate of food availability into their equations are generally less simple to interpret and more variable between sites (Schluter 1988). Abrams (1980) and Wallace (1981) recommended the Schoener Index as the best of the measures of niche overlap when available resources to the organism have not been quantified. Krebs (1989:304-306), referencing Wolda (1981), regarded this measure as one of the better quantitative similarity coefficients available, showing that it is relatively little affected by sample size and number of species (i.e., resources states).

Because percentage of occurrence and percentage of total number of food items tend to over-emphasize the importance of small food items, I used proportions based on total food volume for calculating diet widths and overlaps. Using food volume introduces the possible bias that a large prey item in a single large piranha might overshadow all other items when pooling stomach contents data. However, this problem is overcome to a large extent by dividing fish into different size classes and treating each size class as a separate "trophic unit" (sensu Stoner and Livingston 1984).

In my analysis of diets, the similarity or resemblance matrix generated from the Schoener Index was used as a basis to cluster species using the unweighted pair-group method using mathematical averages, or UPGMA. I used 2 x 2 contingency table X^2 tests (one-tailed) and Mann-Whitney U-tests to test the prediction that forest populations fed more on plant material than their savanna counterparts.

Nutrient Content Analysis of Food Items

In order to compare nutrient values, analyses were carried out to determine ash, crude protein, total fat, carbohydrate, and energy contents of different food items. Three types of food items were examined: small whole fish, fish fins, and fish scales. I also searched the literature for information on the nutrient value of other types of general food items, for example insects and various types of plant material. Prey fishes used for analysis were taken from the Apure River drainage, Venezuela, using cast nets and seines during the dry season in December 1989 and March 1990. Tissues from members of two unrelated families of fishes were tested: (1) Curimatidae, represented by *Curimatella immaculata*, *Cyphocharax spilurus*, and *Steindachnerina argentea*; and (2) Cichlidae, *Aequidens pulcher* and *Cichlasoma orinocense*. These species are common in the Orinoco River basin and are frequently preyed upon by juvenile and adult piranhas.

In total, 135 small cichlids (SL range 39-77 mm) and 96 curimatids (SL range 45-78 mm) were used for nutrient content determinations. Fish were placed on ice immediately after capture, transported to the laboratory at the Universidad de Los Llanos Occidentales (UNELLEZ) in Guanare, Venezuela, and refrigerated until analysis was conducted. Body scales were removed from partially frozen specimens with a small fish scaler, and no attempt was made to clean off the body's outer mucous layer. Only caudal and dorsal fins were used for fin samples; these were removed by clipping with scissors above the fin base to avoid scales. Two or three entire cichlid and curimatid specimens

were used for tests as small whole fish. All subsequent nutrient analyses were carried out at UNELLEZ under the direction of the biochemist Dr. Margioly de Morales. Samples were oven-dried to constant weight at 60 °C to prevent lipids in the body tissues from volatilizing. After drying, samples were ground in a Willey mill and stored in desiccators. Unless otherwise stated, methods of analysis used follow AOAC (1980) guidelines. Results are expressed as percentages of dry weight, rather than as percentages of ash-free dry weight (i.e., on organic matter basis), for ease of comparison to previously published data. All measurements were duplicated; the differences between replicate subsamples of a particular food item were generally less than 1%. Ash contents were determined by combustion of samples of dried body tissue at 550 °C for 3 hours (Pierce et al. 1980). Total fat content was determined by extracting lipids for four hours with diethyl ether. Crude protein was determined by the Kjeldahl method for nitrogen, where crude protein is total nitrogen concentration multiplied by 6.25. Carbohydrates were determined as the sum of crude fiber and nitrogen-free extract; total carbohydrates are the sum of both values. Energy content was measured using a Parr bomb calorimeter and expressed as kJ per g; this can be converted to kilocalories per g by dividing by 4.184.

Intestine Length

Length of the intestinal tract (IL) was determined by removing the entire gastrointestinal tract, placing the extended intestine (without stretching) on a flat surface, and measuring the distance from the pylorus to the anus (Ribble and Smith 1983). Fecal material was left in the intestine during measurement. Relative intestine length for each fish was calculated by dividing IL by standard length (SL). An analysis of covariance (ANCOVA) was carried out in order to compare the regression lines of IL versus SL among species. A Spearman rank correlation test was used to test for an association between relative intestine length and the percent volume of plant material among the

different species. My data indicated allometric changes in intestine length. In order to reduce variation and make comparisons more valid, only specimens ≥ 80 mm SL were used in correlation analysis.

Field and Aquarium Observations

I made qualitative and quantitative observations on the feeding behaviors of wild-caught juvenile and subadult piranhas maintained live in aquaria or large outdoor concrete tanks (L. Nico, unpublished data). Species represented from low Llanos populations were *Pygocentrus caribe*, *Serrasalmus elongatus*, *S. irritans*, *S. medinai*, *S. rhombeus*, and *Pristobrycon striolatus*; those from upper Orinoco sites were *Pygopristis denticulatus* and *Serrasalmus manueli*. In the field, most observations of piranha feeding behavior were done from shore or from boats while fishing, these qualitative observations totaled over one hundred hours. I also made brief underwater observations on the feeding behavior of several species totaling about five hours. Underwater observations were made using mask and snorkel in clearwater and blackwater streams in the states of Bolivar, Guarico, and Monagas. Species observed were juveniles or subadults of *Serrasalmus irritans*, *S. medinai*, *S. rhombeus*, and *Pygocentrus caribe*.

Statistical Analyses

All nonparametric tests were run using the computer software program Basic Statistical Subroutines by DYNACOMP (1983) following Siegel (1956) and Siegel and Castellan (1988). Statistical tests of ANCOVA were done using the SuperANOVA program on a Macintosh SE/30 computer. For cluster analysis, I used the computer program NTSYS-pc (Numerical Taxonomy and Multivariate Analysis System) version 1.5 by Rohlf (1988). Cluster analysis has been shown to be a useful and reliable multivariate

procedure for identifying feeding patterns in assemblages of fishes (Stoner and Livingston1984, Henderson and Walker 1986) and other vertebrates (Jaksíc and Medel 1990). The method has also been used extensively to describe fish distribution patterns (Hocutt and Wiley 1986). Basically, the UPGMA clustering technique generates a hierarchical tree, or dendrogram, grouping together those samples or objects that are most similar. UPGMA is widely applied because it can be used with a variety of resemblance coefficients and also because it forms clusters in a more conservative manner than many other clustering methods (Gauch 1982:199, Romesburg 1984, James and McCulloch 1990:147). As a measure of secondary validity, an additional clustering technique, complete linkage (farthest neighbor), was used to assess whether resulting clusters were more-or-less real rather than mathematical artifacts (Gauch 1982, Romesburg 1984).

CHAPTER 4
COMPOSITION OF PIRANHA ASSEMBLAGES

In this chapter I compare the species composition of piranha assemblages from the low Llanos to those from the upper Orinoco. I also examine and compare species composition and richness among the nine drainages sampled, and present possible habitat correlates. Little has been published on the distribution of Orinoco River fishes, with the upper Orinoco being that part of the basin least explored ichthyologically. Because sampling effort was not equal among all the drainages, I supplemented my data with information from museum collections and published records. Although additional collecting will likely add a few species to faunal lists for several of the drainages, the data presented represent a first attempt at understanding piranha distribution patterns and habitat preferences.

Figure 4-1 is a schematic representation showing the relative distances among drainages in relation to their confluence with the main channel of the Orinoco River. Table 4-1 is based on my samples supplemented by museum material, and shows the species composition by region and drainage. A total of eleven piranha species were taken from the two regions studied. Since 1979, ten species have been collected from the low Llanos of Apure State, whereas my 1989-1991 samples indicate that at least eight species occur in the upper Orinoco of the Amazon Territory of Venezuela. Seven species were widely distributed and inhabited both regions. The Coefficient of Biogeographic Resemblance (CBR) value comparing piranha species composition between the low Llanos and the upper Orinoco was 0.78.

Piranha assemblages in five of the six upper Orinoco drainages were numerically dominated by either *S. rhombeus* or *S. manueli*, or both. The exception was the Mavaca

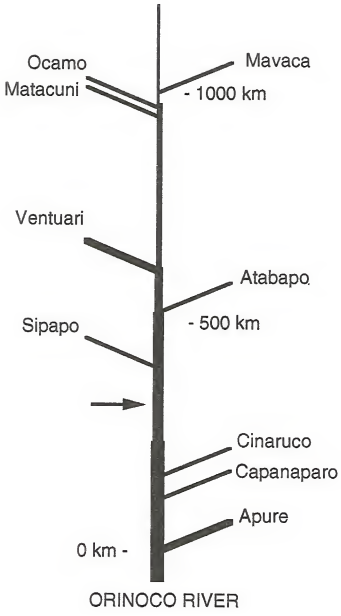


Fig. 4-1. Schematic representation showing relative distances among the nine sampled drainages and their approximate location along Orinoco River main channel. Arrow indicates division between upper and lower Orinoco.

Table 4-1. Occurrence of piranha species in samples from nine drainages in the Orinoco River basin, Venezuela. C = common in fish samples, P = present but uncommon in samples. Data based on my samples and MCNG material unless otherwise indicated.

	River Drainages									
	Low LLanos			Upper Orinoco						
Species	Apure	Capanaparo	Cinaruco	Sipapo	Atabapo	Ventuari	Matacuni	Ocamo	Mavaca	Totals
Serrasalmus medinai	C									1
Serrasalmus irritans	C	P								2
Serrasalmus elongatus	P	P	P							3
Pygocentrus caribe	C	P				P		P		4
Pygopristis denticulatus	P	P	P		P	P			P	6
Serrasalmus manueli		P	C	P	C	C				5
Pristobrycon sp.					P					1
Serrasalmus rhombeus	P	C	C			C	C	C	P	7
Pristobrycon striolatus	P	P	P		pa	P		P	P	7
Serrasalmus altuvei	P						P	P	P	4
Serrasalmus cf. *eigenmanni*			P			P	P	P	C	5
Total number of species	8	7	6	1	4	6	3	5	5	

a = Single specimen from Atabapo River drainage was recorded by Machado-Allison et al. (1989).

River, where *Serrasalmus* cf. *eigenmanni* was the most common piranha collected. *Pygocentrus caribe* is the predominant piranha throughout most of the Llanos, and was abundant in samples from the Apure River drainage although absent or uncommon in the Cinaruco and Capanaparo. *Pygocentrus caribe* was rare in the upper Orinoco. *Serrasalmus irritans* and *S. medinai* were locally common in the low Llanos, but neither was taken in the upper Orinoco. *Serrasalmus manueli*, although absent from much of the Llanos, was commonly taken along with *S. rhombeus* in the Cinaruco River. *Pristobrycon striolatus*, although widespread, was never common in any one drainage.

Species occurred in one to seven of the nine drainages sampled (Table 4-1); most were found in several (mean = 4.1) drainages, with *Serrasalmus rhombeus* and *Pristobrycon striolatus* (taken in seven drainages) being the most widespread. Several species were absent from two middle drainages, the Sipapo and Atabapo rivers. Two species were limited to single drainages. In the Orinoco River basin, *Pristobrycon* sp. is known only from the Atabapo drainage. *Serrasalmus medinai* was represented only in Apure River samples (although it is found in other Orinoco tributaries that fringe the Llanos, drainages not included in this study).

The number of piranha species per drainage ranged from 1 to 8 (mean = 5.0) (Table 4-1). Sipapo drainage samples yielded only one piranha species (*Serrasalmus manueli*), whereas all other drainages were inhabited by three or more species. The Apure had the highest number of species (eight), but it was also the largest and best sampled drainage. There was a significant correlation between numbers of piranha species and size of drainage area (Spearman rank correlation, $r_s = 0.67$, one-tailed $P < .05$, $n = 9$; Table 4-2, Fig. 4-2).

Species composition of piranha assemblages across drainages was highly variable; CBR values ranged from 0 (i.e., no species in common) to 0.83 (Table 4-2). Adjacent drainages often shared many of the same species (Table 4-3), but waterways that had many species in common (i.e., high CBR) were not always those drainages that were

geographically close (Fig. 4-3, Table 4-2). For instance, the Mavaca and Cinaruco were somewhat similar in terms of species composition (CBR = 0.73), yet the two drainages are far apart geographically. Similarly, the Apure drainage had four species in common with the Ocamo, even though these two rivers are separated by roughly 1000 km of waterway (Fig. 4-1). As expected, there was a significant negative correlation between species composition resemblance (i.e., CBR) and the distance between adjacent drainages (r_s = - 0.66, one-tailed $P < .05$, $n = 8$; Table 4-2, Fig. 4-3). However, the relationship was not significant at the 0.05 level when plotting all possible combinations of drainage-pair distances against their CBR values (r_s = - 0.23, one-tailed, $.10 > P > .05$, $n = 36$; Table 4-2, Fig. 4-4).

Figure 4-5 summarizes results of a UPGMA cluster analysis showing affinities among the nine drainages based on CBR similarity values given in Table 4-3. In addition to similarity in species composition, most resulting groups of drainages were related by either geographic proximity, characteristics of the drainage (e.g., water type), or some combination of these two factors. The first major cluster consisted of the three savanna drainages (Capanaparo, Cinaruco, and Apure) and one upper Orinoco tributary (Ventuari). The Capanaparo and Cinaruco are adjacent drainages and both were classified as blackwater, but each receives high input from clearwater streams. The Apure River is a whitewater river with many small blackwater and clearwater tributaries. The Ventuari also is mainly a whitewater river although it has several large blackwater and clearwater tributaries. The second major cluster was formed by three drainages in the upper Orinoco. This cluster consisted of the Matacuni, Ocamo, and Mavaca; all are whitewater rivers and geographically close. The remaining two drainages, the Sipapo and Atabapo, did not cluster with any of the other drainages. They were blackwater rivers with relatively few piranha species. Clustering based on the farthest neighbor strategy resulted in drainage groupings identical to that of the UPGMA method.

Table 4-2. Distance between drainages and Coefficient of Biogeographic Resemblance (in parenthesis) among nine sampled drainages in the Orinoco River basin. Distances measured in kilometers between drainage mouths by way of Orinoco River main channel. CBR values range from 0 (no species in common) to 1 (complete similarity in species composition)

	River Drainages								
	Low Llanos			Upper Orinoco					
	Apu	Cap	Cin	Sip	Ata	Ven	Mat	Oca	Mav
Drainage area (km^2 x 10^3)	167	35	25	13	9.4	40.5	10.1	9.8	5.3
Number of piranha species	8	7	6	1	4	6	3	5	5
Apure		110 (0.80)	160 (0.57)	400 (0)	530 (0.33)	610 (0.57)	945 (0.36)	965 (0.62)	1000 (0.62)
Capanaparo			50 (0.77)	290 (0.25)	420 (0.55)	500 (0.77)	835 (0.20)	855 (0.50)	890 (0.50)
Cinaruco				240 (0.29)	370 (0.60)	450 (0.83)	785 (0.44)	805 (0.55)	840 (0.73)
Sipapo					130 (0.40)	210 (0.29)	545 (0)	565 (0)	600 (0)
Atabapo						80 (0.60)	415 (0)	435 (0.22)	470 (0.44)
Ventuari							335 (0.44)	355 (0.73)	590 (0.73)
Matacuni								20 (0.75)	55 (0.75)
Ocamo									35 (0.80)
Mavaca									

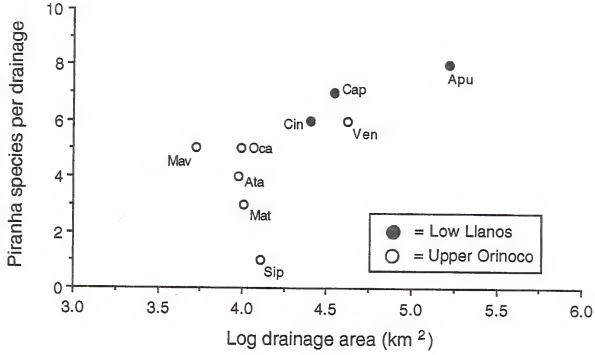


Fig. 4-2. Scatter diagram showing relationship between number of piranha species per drainage and log of the drainage area size (km^2) for nine sampled drainages in Orinoco River basin, Venezuela. Drainage abbreviations are: Apu = Apure, Ata = Atabapo, Cap = Capanaparo, Cin = Cinaruco, Mat = Matacuni, Mav = Mavaca, Oca = Ocamo, and Sip = Sipapo.

Table 4-3. Number of shared piranha species and Coefficient of Biogeographic Resemblance (CBR) (in parenthesis) among nine sampled drainages in the Orinoco River basin. CBR values range from 0 (no species in common) to 1 (complete similarity in species composition).

	River Drainages								
	Low Llanos			Upper Orinoco					
	Apu	Cap	Cin	Sip	Ata	Ven	Mat	Oca	Mav
Number of piranha species	8	7	6	1	4	6	3	5	5
Apure		6 (0.80)	4 (0.57)	0 (0)	1 (0.33)	4 (0.57)	2 (0.36)	4 (0.62)	4 (0.62)
Capanaparo			5 (0.77)	1 (0.25)	2 (0.55)	5 (0.77)	1 (0.20)	3 (0.50)	3 (0.50)
Cinaruco				1 (0.29)	2 (0.60)	5 (0.83)	2 (0.44)	3 (0.55)	4 (0.73)
Sipapo					1 (0.40)	1 (0.29)	0 (0)	0 (0)	0 (0)
Atabapo						2 (0.60)	0 (0)	0 (0.22)	1 (0.44)
Ventuari							2 (0.44)	4 (0.73)	4 (0.73)
Matacuni								3 (0.75)	3 (0.75)
Ocamo									4 (0.80)
Mavaca									

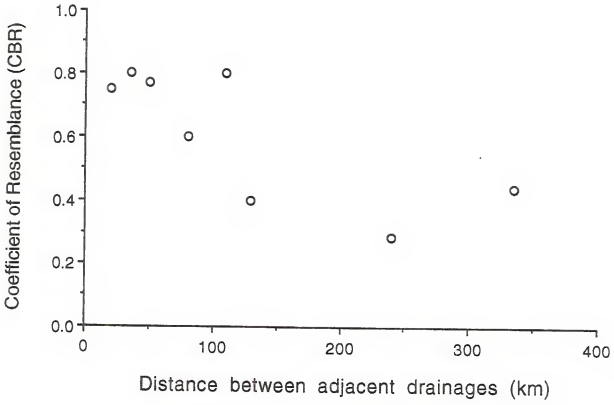


Fig. 4-3. Scatter diagram showing similarity in piranha species composition between adjacent sampled drainages versus distance between adjacent drainages. Similarity measure was Duellman's (1990) Coefficient of Biogeographic Resemblance.

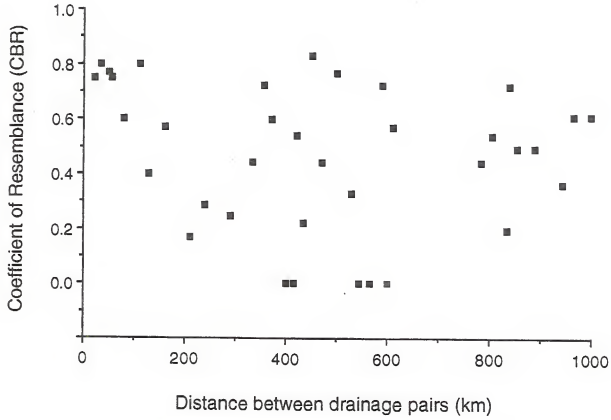


Fig. 4-4. Scatter diagram showing similarities in piranha species composition between all possible paired drainages and the distance between paired drainages. Similarity values and distances are from Table 4- 2.

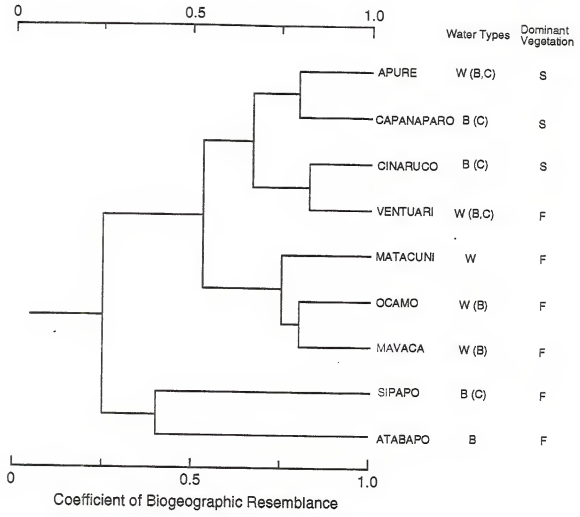


Fig. 4-5. Dendrogram from cluster analysis depicting similarities among nine sampled drainages of Orinoco River basin based on piranha species composition. Major and minor (in parenthesis) water types, W = whitewater, B = blackwater, and C = clearwater; Dominant regional flora, S = savanna (low Llanos), and F = forest (upper Orinoco). Similarity values are from Table 4-3. Clustering technique was UPGMA, and similarity measure was Duellman's (1990) Coefficient of Biogeographic Resemblance.

A summary of species occurrence by habitat type is given in Table 4-4. Most species were found in a variety of environmental conditions, but relative abundances differed among sites. *Serrasalmus rhombeus* and *S. manueli* were frequently taken in riverine habitats; other piranhas were more common in floodplain habitats (e.g., lagoons or old meanders) and in caños with slow currents. In those cases where piranhas were found in large streams or rivers, they commonly congregated in adjoining slackwaters near the interface between fast-flowing and still waters, for example near the mouths of sloughs or deep caños.

Most piranhas were found in two or all of the three major water types (Table 4-4), but greatest numbers occurred in whitewater habitats. Three species (i.e., *Serrasalmus manueli*, *Pygopristis denticulatus*, and *Pristobrycon* sp.) were usually associated with low-pH, blackwater habitats . Nevertheless, most species seem to tolerate a wide range of temperatures and pH, as shown by wild-caught juveniles of both *S. manueli* and *P. denticulatus* that have survived nine months (to date) in aquarium water with pH as high as 8.5. Water temperatures at sample sites ranged from 24.5 to 38 °C, and pH 4.5 to 7.2; water transparency ranged from very turbid (10 cm as measured with a Secchi disk), to very clear (>3 m).

Where piranhas occur, two or more species are commonly taken together. In the low Llanos, juveniles and subadults of as many as five species (i.e., *Pygocentrus caribe*, *Serrasalmus altuvei*, *S. irritans*, *S. medinai*, and *S. elongatus*) were occasionally taken in single seine hauls in floodplain pools of the Apure drainage. In the upper Orinoco, adults of as many as four species of piranha (e.g., *Serrasalmus rhombeus*, *S.* cf. *eigenmanni*, *Pygocentrus caribe*, and *Pristobrycon striolatus*) were caught together in gill nets set during evening twilight. Sites of highest species richness were characterized by a large amount of instream cover or other protection, including mats of aquatic vegetation, adjacent flooded forest, or deep water. Small juvenile piranhas (<40 mm SL) were only found in

microhabitats where there was high cover provided by herbaceous plants. In the Llanos, small piranhas relied on water hyacinth or flooded grasses for shelter and as a foraging place. In the upper Orinoco, young juveniles were limited to a few sites where there were mats of flooded grasses (e.g., stream edges) or shallow waters with dense growths of submergent plants, such as beds of the aquatic plant *Elodea*.

Table 4-4. Summary of species occurrence by habitat and water type, based on samples in Orinoco River basin, Venezuela. Physico-chemical data represent minimum-maximum values recorded for water at capture sites. Transparency measured with Secchi disk.

Species	Habitat Type					Water Type			Physico-Chemical Ranges		
	Big River	Stream	Lagoon/ Oxbow	Flooded-forest	Flooded-savanna	White	Clear	Black	pH	Temperature (°C)	Transparency (m)
Pygocentrus caribe	X	X	X	X	X	X	X	X	6-7	26-30	0.1->2.0
Pristobrycon striolatus		X	X	X	X	X	X	X	6-6.7	27.5-30.5	0.5-1.0
Pristobrycon sp.		X		X				X	4.5	27	~2
Pygopristis denticulatus		X	X		X			X	4.5-6	26-38	1-2
Serrasalmus altuvei		X	X		X	X		X	6-7.2	24.5-31	0.1-1.0
Serrasalmus cf. *eigenmanni*	X	X	X	X	X	X		X	6-7	25-33	0.5-0.9
Serrasalmus elongatus		X	X		X	X		X	6-6.5	29-29.5	0.1->2.0
Serrasalmus irritans		X	X		X	X	X	X	6-7	27-29.5	0.1->2.0
Serrasalmus manueli	X	X	X	X	X	X		X	4.5-6.5	24.5-31	0.7-2.3
Serrasalmus medinai		X	X		X	X	X	X	6-7	27-33	0.1-1.0
Serrasalmus rhombeus	X	X	X		X	X	X	X	6-7.2	24.5-31	0.1->2.0

Note: Physico-chemical parameters not measured at all sites, therefore ranges given in many cases are probably conservative.

CHAPTER 5
TROPHIC ECOLOGY OF SAVANNA PIRANHAS: THE APURE DRAINAGE

This chapter focuses on the diets of piranhas from the area around the Fernando Corrales ranch and research station of the University of the Western Llanos (UNELLEZ), located in the Caño Caicara region, Apure River drainage, in the low Llanos (Fig. 5-1). I give this drainage separate treatment because it is the only site where long-term sampling (1979-1990) has been carried out (Taphorn and Lilyestrom 1984, Nico and Taphorn 1984, 1985, 1988, Nico 1990, Taphorn 1990). The existing data base on piranhas from the Caño Caicara region is the most complete of any single locality or drainage in the Orinoco basin. The seven species examined were *Pygocentrus caribe*, *Serrasalmus altuvei*, *S. medinai*, *S. elongatus*, *S. irritans*, *S. rhombeus*, and *Pristobrycon striolatus* (Fig. 5-2). I also report on the diet of the serrasalmine *Catoprion mento*, a close relative of the piranhas.

Study Area

The study area is located in the low Llanos of Apure State (07°25'50"N, 69°35'30"W) about 80 km W of the town of Mantecal (Fig. 5-1). Several permanent streams border the 12,600-ha ranch, caños Caicara, Maporal, and Guaritico. These low-gradient streams have mostly silty bottoms, and are bordered by narrow gallery forests. The ranch is maintained primarily for grazing of cattle and encompasses open flat savanna with a very gradual sloping terrain west to east. Most of the savanna floodplain of the ranch is surrounded by a 2.5 m high earthen dike constructed to control flooding during the rainy season and hold water during the drier part of the year. During the rains most of the

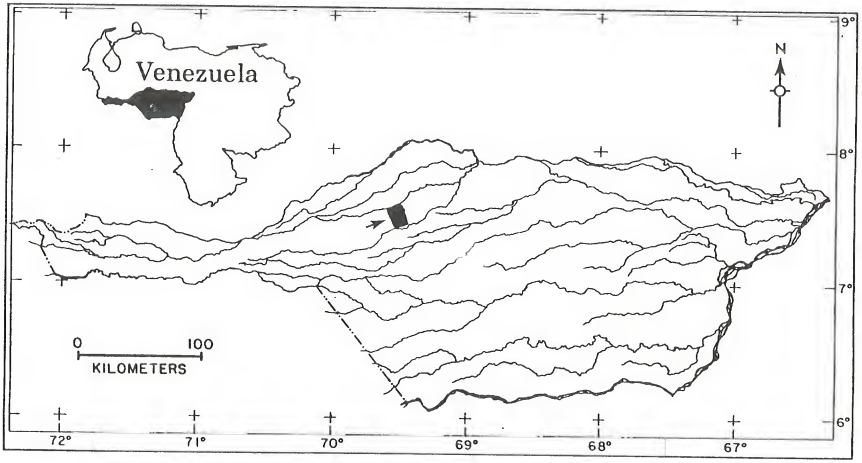


Fig. 5-1. Location of Caño Caicara study area, Apure Drainage, in low Llanos of Apure State, Venezuela. (Arrow indicates Fernando Corrales ranch and research station of UNELLEZ).

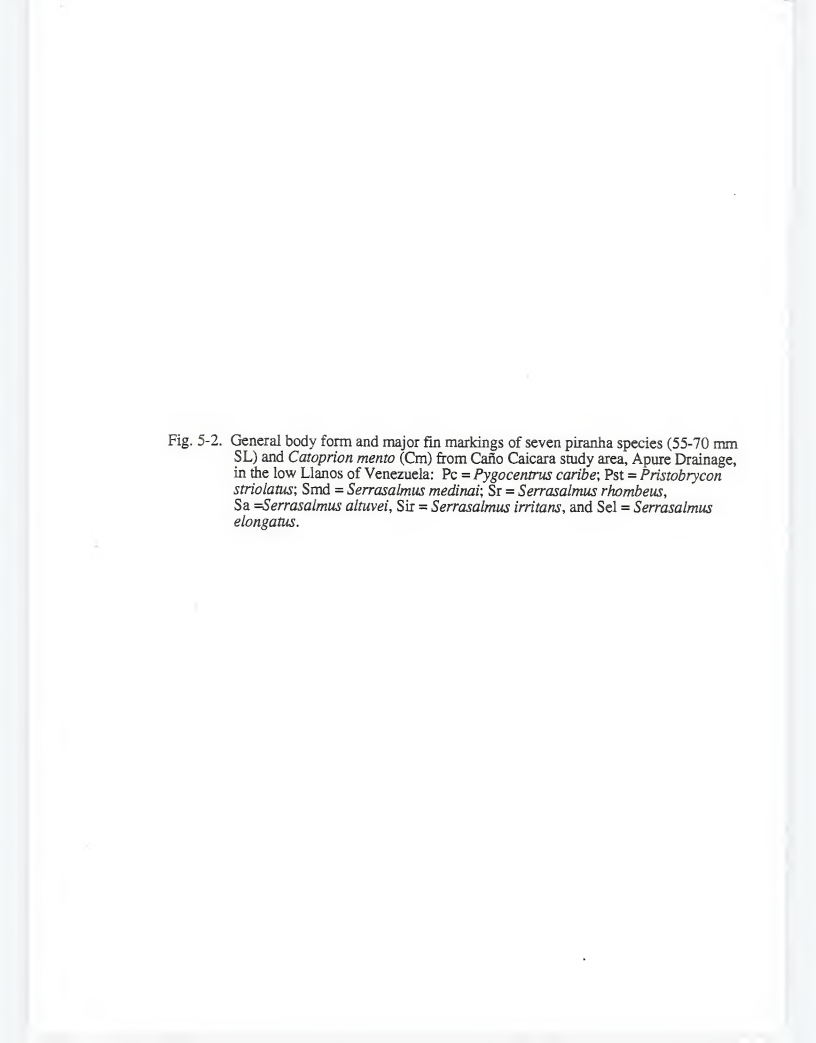
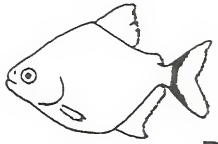


Fig. 5-2. General body form and major fin markings of seven piranha species (55-70 mm SL) and *Catoprion mento* (Cm) from Caño Caicara study area, Apure Drainage, in the low Llanos of Venezuela: Pc = *Pygocentrus caribe*; Pst = *Pristobrycon striolatus*; Smd = *Serrasalmus medinai*; Sr = *Serrasalmus rhombeus*, Sa =*Serrasalmus altuvei*, Sir = *Serrasalmus irritans*, and Sel = *Serrasalmus elongatus*.

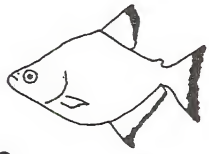
Pc



Pst

Smd

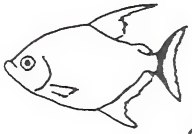
Sr



Sa

Sir

Sel



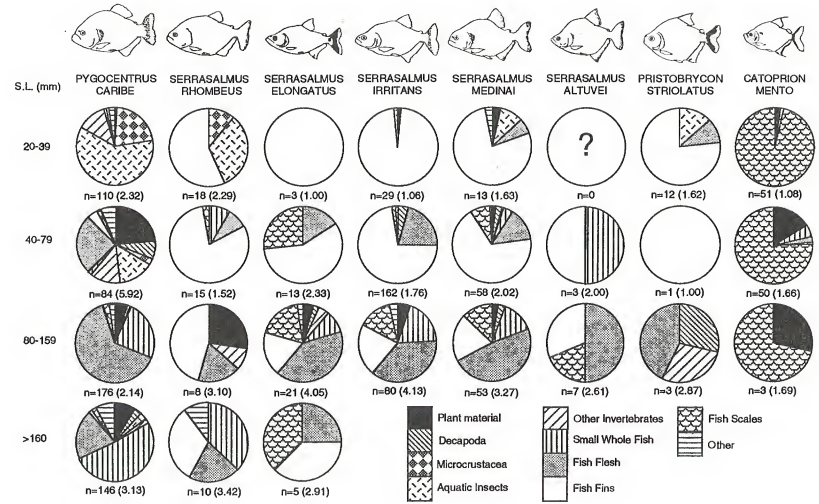
Cm

savanna becomes flooded, with low areas covered by as much as 2 m of water. Lower areas and deeper borrow pits contain water throughout the year, but most permanent water sites are reduced to less than 1 m depth during the dry season. The fish species composition of borrow pits resembles that of natural lagoon habitats. Large free-floating mats of vegetation, primarily *Eichhornia crassipes* and *E. azurea*, are common in streams and savanna pools. During high water, fishes can move between the streams and the interior of the diked areas through culverts or low sections of the dike, but this interchange has been greatly reduced as dike stability has been achieved. During the late dry season (January to early April), the streams have little or no flow and are often reduced to isolated pools. Rainy season flow is continuous with depths to 5 m or more. Width ranges from 3 to 12 m during low water to over 30 m during peak flooding. Although the Apure River itself is white water in character, streams of the study area are essentially blackwater habitats with low transparency. The flooded savanna pools are white water habitats, usually very turbid (<10 cm Secchi disk), but the larger pools often become quite clear (>1 m Secchi disk) late in the rainy season.

Species Accounts

In this section, I describe the general morphology, local distribution and habitat, and the diets of the piranha species found in the Caño Caicara study area. Information on the smallest size class of piranhas, juveniles less than 20 mm SL, were pooled; all were tentatively identified as *Pygocentrus caribe*. Figure 5-3 is a summary of the diets by size class (Group II and larger) of the seven piranhas and *Catoprion mento* from the Caño Caicara area.

Fig. 5-3. Diets by size class of seven piranha species and *Catoprion mento* from Caño Caicara study area, Apure River drainage, in the low Llanos of Venezuela. Size of segments represents percentage of adjusted volume (V_a) of each prey type; n = number of stomachs examined; numbers in parentheses represent diet breadth using formula of Levins (1968).


S.L. (mm)
PYGOCENTRUS CARIBE
SERRASALMUS RHOMBEUS
SERRASALMUS ELONGATUS
SERRASALMUS IRRITANS
SERRASALMUS MEDINAI
SERRASALMUS ALTUVEI
PRISTOBRYCON STRIOLATUS
CATOPRION MENTO
20-39
40-79
80-159
>160
?
n=110 (2.32)
n=18 (2.29)
n=3 (1.00)
n=29 (1.06)
n=13 (1.63)
n=0
n=12 (1.62)
n=51 (1.08)
n=84 (5.92)
n=15 (1.52)
n=13 (2.33)
n=162 (1.76)
n=58 (2.02)
n=3 (2.00)
n=1 (1.00)
n=50 (1.66)
n=176 (2.14)
n=8 (3.10)
n=21 (4.05)
n=80 (4.13)
n=53 (3.27)
n=7 (2.61)
n=3 (2.87)
n=3 (1.69)
n=146 (3.13)
n=10 (3.42)
n=5 (2.91)
Plant material
Decapoda
Microcrustacea
Aquatic Insects
Other Invertebrates
Small Whole Fish
Fish Flesh
Fish Fins
Fish Scales
Other

Pygocentrus caribe (Valenciennes 1849)

Pygocentrus caribe was the most abundant piranha in the Caño Caicara area, occurring in both flooded savanna and flowing waters. This blunt-headed, heavy-bodied species (Fig. 5-2) reaches approximately 300 mm SL. Stomach contents of 516 *P. caribe* in the four larger size classes are given in Table 5-1 and Figure 5-3. Unlike most other piranha species, fish fins and scales were of minor importance in stomachs of juveniles. Group II fish fed most heavily on aquatic insects, followed by microcrustaceans, but for Group III fish flesh was the most important food item, followed by plant material (primarily vascular plant debris) and aquatic insects. Larger *P. caribe* of groups IV and V took mostly fish flesh and whole small fish.

Thirty-two species of prey fishes (mostly characins) were identified from stomachs of Groups IV and V *P. caribe* (Table 5-2). There were also several instances of cannibalism by adults on small juveniles. In addition to fish, larger juveniles and adults sometimes ate other vertebrates, perhaps as carrion. Different stomachs contained a chunk of flesh from a small caiman (*Caiman crocodilus*), skin of a lizard (probably *Ameiva*), and a small adult leptodactylid frog. Three individuals taken together had stomachs full of feathers, flesh, and bone fragments of a white-faced whistling duck (*Dendrocygna viduata*). Mammals were not found in *P. caribe* from the study area, but I have found flesh and fur of small rodents in specimens from nearby localities.

Serrasalmus irritans Peters 1877

Serrasalmus irritans was very common, usually second only to *P. caribe* in numbers of individuals at most sampling sites. My sample consisted of 271 specimens (Table 5-3 and Fig. 5-3). It has a moderately pointed snout (Fig. 5-2) and is seldom longer than 160 mm SL. My study shows that juvenile *S. irritans* (Groups II and III) specialized on fins of other fishes. Stomachs of the young of this piranha were typically packed exclusively with fins, mostly from fish smaller or similar in size to the predator.

Table 5-1. Food items of *Pygocentrus caribe* from the Apure River drainage (Caño Caicara area) by size class. %O = percent frequency of occurrence; %D = percent dominance; and $\%V_a$ = percent adjusted volume. N = 516.

Size class (mm, SL)	II (20-39)			III (40-79)			IV (80-159)			V (≥160)		
Number examined	110			84			176			146		
Number empty	1			5			18			46		
Food items	%O	%D	$\%V_a$	%O	%D	$\%V_a$	%O	%D	$\%V_a$	%O	%D	$\%V_a$
Plant material	17.4	1.8	1.1	43.0	25.3	23.5	29.7	8.7	5.4	41.0	15.0	8.8
Decapoda	-	-	-	10.1	7.2	7.4	3.8	1.2	1.2	9.0	4.7	3.0
Microcrustaceans	78.0	23.7	21.4	19.0	3.6	2.6	-	-	-	-	-	-
Aquatic insects	80.0	55.3	60.7	32.9	14.5	14.7	0.6	-	-	11.0	4.7	3.0
Other invertebrates	36.7	14.0	12.3	30.4	10.8	12.4	5.1	1.2	0.6	21.0	4.7	2.0
Small whole fish	0.9	0.9	1.1	2.5	1.2	1.8	29.1	22.0	24.1	51.0	41.1	51.0
Fish flesh	0.9	0.9	1.1	29.1	19.3	25.3	81.6	59.0	63.7	38.0	17.8	20.5
Fish fins	-	-	-	36.7	8.4	4.1	12.0	0.6	0.3	7.0	2.8	1.8
Fish scales	-	-	-	17.7	2.4	1.8	12.0	4.6	2.8	12.0	3.7	2.0
Other	3.7	3.5	2.4	10.1	7.2	6.5	5.1	2.9	1.9	9.0	5.6	7.8

Table 5-2. List of vertebrate prey taxa identified from the stomach contents of the four most common piranhas from the Caño Caicara area, Apure River drainage, in the low Llanos of Venezuela.

Species	Vertebrate Prey (frequency of occurrence)
Pygocentrus caribe	Fish (whole or flesh): Characidae - *Aphyocharax erythrurus* (6), *Astyanax bimaculatus* (1), *Astyanax* sp. (3), *Charax* sp. (2), *Cheirodon pulcher* (1), *Ctenobrycon spilurus* (22), *Gymnocorymbus thayeri* (15), *Hemigrammus marginatus* (5), *Hemigrammus* sp. (5), *Moenkhausia dichroura* (2), *Odontostilbe pulcher* (7), *Poptella orbicularis* (6), *Pygocentrus caribe* (6), and *Roeboides affinis* (1), *Roeboides dayi* (8), *Roeboides* sp. (3), *Serrasalmus eigenmanni* (1), *Serrasalmus* sp. (1), *Triportheus* sp. (1); Curimatidae - *Curimata metae* (10), *curimatids* (14); Lebiasinidae - *Pyrrhulina* cf. *lugubris* (2); characoid (8); Cichlidae - *Microgeophagus ramirezi* (2), Gymnotidae - *Gymnotus carapo* 1); Sternopygidae - *Sternopygus macrurus* (1), and *Eigenmannia* spp. (10); Hypopomidae - *Hypopomus* sp. (1); Auchenipteridae - *Entomocorus gameroi* (1) and *Parauchenipterus galeatus* (1); Pimelodidae - *Pimelodella* sp.(1); Callichthyidae - *Hoplosternum littorale* (1); Rivulidae (1). Fins of Hypophthalmidae - *Hypophthalmus* cf. *edentatus* (1): Characidae - *Triportheus* sp. (1). Reptiles: Flesh of *Caiman crocodilus* (1); flesh of lizard, probably *Ameiva* (1). Amphibians: Small adult leptodactylid frog. Birds: Feathers and flesh of white-faced whistling duck (*Dendrocygna viduata)* (3).
Serrasalmus irritans	Fish (whole or flesh): Characidae - *Ctenobrycon spilurus* (1), *Odontostilbe pulcher (2), Hemigrammus* sp.(1), small juvenile *Pygocentrus caribe* (1); Curimatidae - *Curimata metae* (1), curimatid (1); characoid (4); gymnotoid (1); Cichlidae - *Microgeophagus ramirezi* (1), cichlid (1). Fins of adult *Pygocentrus caribe (2).*
Serrasalmus medinai	Fish (whole or flesh): Characidae - *Aphyocharax erythrurus* (1), *Hemigrammus marginatus* (2), Hemigrammus sp. (1), and *Odontostilbe pulcher* (2), characid (2); Curimatidae - *Curimata metae (2), curimatid (1);* Cichlidae - *Microgeophagus ramirezi* (1); gymnotoid (1); catifish (1); Fins from Loricariidae (1).
Serrasalmus rhombeus	Fish (whole or flesh): Characidae - *Astyanax bimaculatus* and *Charax* sp.(1), characid (1); characoid (1); Doradidae - *Agamyxis*? (3); unidentified catfish (1); Fins of Characidae - *Pygocentrus caribe (1);* Erythrinidae? (1). Amphibians: Small adult frog (1).

Table 5-3. Food items of *Serrasalmus irritans* from the Apure River drainage (Caño Caicara area) by size class. %O = percent frequency of occurrence; %D = percent dominance; and $\%V_a$ = percent adjusted volume. N = 271.

Size class (mm, SL)	II (20-39)			III (40-79)			IV (80-159)		
Number examined	29			162			80		
Number empty	1			7			10		
Food items	%O	%D	$\%V_a$	%O	%D	$\%V_a$	%O	%D	$\%V_a$
Plant material	10.7	3.6	1.4	1.9	-	-	18.6	8.3	5.0
Decapoda	-	-	-	0.6	0.6	0.3	1.4	-	-
Aquatic insects	-	-	-	3.2	-	-	1.4	-	-
Other invertebrates	-	-	-	0.6	-	-	1.4	1.4	0.4
Small whole fish	-	-	-	3.2	3.1	4.0	18.6	13.9	18.8
Fish flesh	-	-	-	21.9	17.5	21.0	28.6	25.0	37.1
Fish fins	92.9	92.6	97.3	81.9	73.8	72.3	37.1	22.2	21.3
Fish scales	10.7	-	-	23.2	3.1	1.3	37.1	23.6	14.2
Other	3.6	3.6	1.4	3.9	1.9	1.2	8.6	5.6	3.3

It was usually not possible to identify the fins eaten, but the thick red anal fins of *Pygocentrus caribe* were found in two individuals. Large *S. irritans* preyed mostly on small whole fish, fish flesh, fins, and occasionally scales. Fishes eaten whole or in pieces by *S. irritans* are given in Table 5-2. A small juvenile *P. caribe* was found in the stomach of one individual. No nonfish vertebrate remains were found.

Serrasalmus medinai Valenciennes 1849

Serrasalmus medinai was the third most common piranha in the study area; 124 specimens were analyzed for diet (Table 5-4 and Fig. 5-3). It is a medium-sized piranha, usually less than 160 mm SL with a head shape that is intermediate between the robust *P. caribe* and species with pointed snouts (Fig. 5-2). Unlike *Pygocentrus*, but similar to other *Serrasalmus*, it has a series of ectopterygoid teeth that is easily seen even in small individuals (from about 25 mm SL). It is primarily a fin-eater when small (20-79 mm SL). The largest individuals (Group IV) fed chiefly on fish flesh, fins and scales, and small whole fish. Prey fish identified from the stomachs of *S. medinai* are given in Table 5-2. The only fin identified was from an armored catfish. Shrimp and crabs were also eaten.

Serrasalmus rhombeus (Linnaeus) 1766

Serrasalmus rhombeus was uncommon in flooded savanna of the Caño Caicara study area, although on several occasions adults were taken in large numbers by hook and line at night in Caño Maporal. Juvenile *Serrasalmus rhombeus* have a somewhat elongate body and sharp snout (Fig. 5-2). They resemble *S. irritans* in body form, but are slightly more robust. Adults have heavy rhomboidal bodies. The body and fins of large individuals, some well over 300 mm SL, are black or blue-black, and the iris is often deep red. I examined the stomach contents of 51 *S. rhombeus* from the Caño Caicara area (Table 5-5 and Fig. 5-3).

Table 5-4. Food items of *Serrasalmus medinai* from the Apure River drainage (Caño Caicara area) by size class. %O = percent frequency of occurrence; %D = percent dominance; and $\%V_a$ = percent adjusted volume. N = 124.

Size class (mm, SL)	II (20-39)			III (40-79)			IV (80-159)		
Number examined	13			58			53		
Number empty	0			2			3		
Food items	%O	%D	$\%V_a$	%O	%D	$\%V_a$	%O	%D	$\%V_a$
Plant material	7.7	7.1	3.2	16.1	1.7	1.6	26.0	5.8	2.9
Decapoda	-	-	-	1.8	1.7	2.4	8.0	1.9	2.9
Aquatic insects	7.7	7.1	9.7	-	-	-	-	-	-
Other invertebrates	-	-	-	5.4	1.7	0.8	4.0	-	-
Small whole fish	-	-	-	5.4	3.4	4.0	14.0	9.6	13.7
Fish flesh	7.7	7.1	6.5	23.2	15.3	14.0	46.0	36.5	48.0
Fish fins	84.6	71.4	77.4	80.4	62.7	68.4	66.0	30.8	20.1
Fish scales	-	-	-	44.6	11.9	8.0	36.0	15.4	12.3
Other	7.7	7.1	3.2	1.8	1.7	0.8	-	-	-

Table 5-5. Food items of *Serrasalmus rhombeus* from the Apure River drainage (Caño Caicara area) by size class. %O = percent frequency of occurrence; %D = percent dominance; and $\%V_a$ = percent adjusted volume. N = 51.

Size class (mm, SL)	II (20-39)			III (40-79)			IV (80-159)			V (≥160)		
Number examined	18			15			8			10		
Number empty	1			0			1			1		
Food items	%O	%D	$\%V_a$	%O	%D	$\%V_a$	%O	%D	$\%V_a$	%O	%D	$\%V_a$
Plant material	-	-	-	20.0	-	-	42.9	25.0	27.3	11.1	-	-
Microcrustaceans	23.5	15.8	10.9	-	-	-	-	-	-	-	-	-
Aquatic insects	47.1	26.3	32.6	-	-	-	14.3	-	-	11.1	-	-
Other invertebrates	5.9	-	-	-	-	-	28.6	12.5	9.1	33.3	-	-
Small whole fish	-	-	-	6.7	5.9	8.6	-	-	-	44.4	33.3	36.9
Fish flesh	-	-	-	13.3	11.8	8.6	28.6	12.5	18.2	55.6	22.2	21.1
Fish fins	64.7	57.9	56.5	93.3	76.5	80.0	71.4	50.0	45.5	33.3	33.3	31.6
Fish scales	-	-	-	26.7	5.9	2.9	42.9	-	-	22.2	-	-
Other	-	-	-	-	-	-	14.3	-	-	11.1	11.1	10.5

Juvenile *S. rhombeus* in size classes II-IV specialized on fish fins. Aquatic insects, mostly plecopterans, were packed in the guts of several specimens from Caño Guaritico. The ten largest *S. rhombeus* (Group V) had taken almost equal volumes of whole small fish, chunks of fish flesh, and fish fins. Fishes identified from the stomachs of larger *S. rhombeus* are given in Table 5- 2. Three large *S. rhombeus* collected at night in Caño Maporal contained entire or partial individuals of small 20-30 mm SL doradid catfishes. One individual had eaten a small adult frog.

Serrasalmus elongatus Kner 1860

Serrasalmus elongatus was rare to uncommon in my samples in the study area. It is a pikelike piranha (Fig. 5-2), having the most elongate body, relative to body depth, of all piranhas. I examined 42 individuals, including a few from the small size class (Group II) from other locations in the Apure River drainage (Table 5-6 and Fig. 5-3). Stomachs of three small juveniles (20-39 mm SL) were packed with fins of other small fishes, and one also contained a nematode (possibly a parasite). Stomachs of large specimens contained fish fins and many scales. In addition, small whole fish and chunks of fish flesh were taken by the largest *S. elongatus*.

Serrasalmus altuvei Ramirez 1965

Serrasalmus altuvei was rare in the Caño Caicara area, and was found in both streams and floodplain pools. It is a medium-sized piranha; maximum length in my samples was less than 200 mm SL, with a deep narrow body and a slender pointed snout (Fig. 5-2). It has a silver body and a broad, black terminal band on its unpaired fins, none of my specimens from the Apure drainage had any red on the body. I examined the stomachs of ten of 17 individuals collected in Caño Maporal and the flooded savanna

Table 5-6. Food items of *Serrasalmus elongatus* from the Apure River drainage (Caño Caicara area) by size class. %O = percent frequency of occurrence (nonempty stomachs); %D = percent dominance; and $\%V_a$ = percent adjusted volume. N = 42.

Size class (mm, SL)	II (20-39)			III (40-79)			IV (80-159)			V (≥160)		
Number examined	3			13			21			5		
Number empty	0			0			1			0		
Food items	%O	%D	$\%V_a$	%O	%D	$\%V_a$	%O	%D	$\%V_a$	%O	%D	$\%V_a$
Plant material	-	-	-	23.1	-	-	30.0	5.0	4.5	40.0	-	-
Decapoda	-	-	-	-	-	-	5.0	5.0	2.3	-	-	-
Other invertebrates	33.3	-	-	-	-	-	15.0	5.0	4.5	-	-	-
Small whole fish	-	-	-	-	-	-	10.0	10.0	9.1	20.0	-	-
Fish flesh	-	-	-	15.4	12.5	15.6	35.0	30.0	40.9	80.0	40.0	25.0
Fish fins	100.0	100.0	100.0	76.9	50.0	57.8	40.0	20.0	18.2	40.0	20.0	37.5
Fish scales	-	-	-	84.6	37.5	26.6	50.0	20.0	18.2	80.0	40.0	37.5
Other	-	-	-	-	-	-	5.0	5.0	2.3	-	-	-

(Table 5-7 and Fig. 5-3). Fish fins, scales, flesh and small whole fish were found in the two size classes (III and IV) represented in our samples.

Pristobrycon striolatus (Steindachner) 1908

Pristobrycon striolatus was rare in the Caño Caicara study area, and was collected only on several occasions from Caño Maporal. It is a medium-sized species (Fig. 5-2), less than 200 mm SL; the largest specimen taken from the Caño Caicara region was 156 mm. Adults sometimes had a red-orange chest and occasionally a pattern of orange vertical bars along the sides. *Pristobrycon striolatus* has a rather blunt snout, but smaller and weaker jaws and jaw musculature than *Pygocentrus caribe*. The body is deep and strongly compressed. Small juveniles are similar to young *Serrasalmus rhombeus* but are slightly stouter, lack ectopterygoid teeth, and have little if any side spotting. The largest individual collected in the study area was 159 mm SL. I examined the stomach contents of 16 of the 38 specimens collected. Food items by size class are given in Table 5-8 and Figure 5-3. Specimens in Group II fed mostly on fish fins as did the one Group III specimen examined. Three adults from Group IV contained fish flesh, a few scales, shrimp fragments, an adult aquatic beetle, an aquatic hemipteran and unidentified insect fragments.

Catoprion mento (Cuvier) 1819

Catoprion mento was common in many of the streams and savanna pools. It is a small, deep-bodied species (Fig. 5-2) that is closely related to piranhas. Although maximum size is around 120 mm SL, in the Apure drainage most specimens sampled were under 80 mm SL, and none was greater than 100 mm. The teeth of *C. mento* are somewhat everted and its long lower jaw swings open to more than 180 degrees, making it well suited for scraping scales off other fish. The stomachs of all 104 specimens examined contained fish scales (ranging up to 23 mm in diameter) (Table 5-9 and Fig. 5-3). Plant material, primarily comprising vascular debris and root wads, and occasionally filamentous

Table 5-7. Food items of *Serrasalmus altuvei* from the Apure River drainage (Caño Caicara area) by size class. %O = percent frequency of occurrence; %D = percent dominance; and $\%V_a$ = percent adjusted volume. N = 10.

Size class (mm, SL)	III (40-79)			IV (80-159)		
Number examined	3			7		
Number empty	0			0		
Food items	%O	%D	$\%V_a$	%O	%D	$\%V_a$
Plant material	-	-	-	28.9	-	-
Small whole fish	33.3	33.3	50.0	-	-	-
Fish flesh	33.3	-	-	42.9	30.0	50.0
Fish fins	66.7	66.7	50.0	71.4	40.0	31.3
Fish scales	-	-	-	42.9	30.0	18.8
Other	-	-	-	14.3	-	-

Table 5-8. Food items of *Pristorbrycon striolatus* from the Apure River drainage (Caño Caicara area) by size class. %O = percent frequency of occurrence; %D = percent dominance; and $\%V_a$ = percent adjusted volume. N = 16.

Size class (mm, SL)	II (20-39)			III (40-79)			IV (80-159)		
Number examined	12			1			3		
Number empty	1			0			0		
Food items	%O	%D	$\%V_a$	%O	%D	$\%V_a$	%O	%D	$\%V_a$
Decapoda	-	-	-	-	-	-	66.7	33.3	28.6
Aquatic insects	27.3	18.2	13.3	-	-	-	66.7	-	-
Other invertebrates	3.9	-	-	-	-	-	33.3	33.3	28.6
Fish flesh	18.2	9.1	10.0	-	-	-	33.3	33.3	42.9
Fish fins	81.8	72.7	76.7	100.0	100.0	100.0	-	-	-
Fish scales	-	-	-	-	-	-	33.3	-	-

Table 5-9. Food items of *Catoprion mento* from the Apure River drainage (Caño Caicara area) by size class. %O = percent frequency of occurrence; %D = percent dominance; and $\%V_a$ = percent adjusted volume. N = 104.

Size class (mm, SL)	II (20-39)			III (40-79)			IV (80-159)		
Number examined	51			50			3		
Number empty	0			0			0		
Food items	%O	%D	$\%V_a$	%O	%D	$\%V_a$	%O	%D	$\%V_a$
Plant material	25.0	2.0	2.1	50.0	19.0	16/1	33.3	33.3	28.6
Microcrustaceans	2.0	-	-	-	-	-	-	-	-
Aquatic insects	2.0	-	-	-	-	-	-	-	-
Other invertebrates	3.9	2.0	1.4	-	-	-	-	-	-
Small whole fish	-	-	-	4.0	3.4	5.0	-	-	-
Fish flesh	-	-	-	2.0	1.7	2.5	-	-	-
Fish fins	-	-	-	2.0	1.7	0.8	-	-	-
Fish scales	100.0	96.1	96/4	100.0	74.1	75.6	100.0	66.7	71.4

algae, was present in small amounts in many stomachs. Rare items included an aquatic beetle larva, a cladoceran, and the head of a small characid fish (*Aphyocharax erythrurus*).

Small juvenile piranhas, Group I (10-19 mm SL)

Most piranhas spawn at the onset of the rainy season. Small juveniles inhabit the flooded grasses and marsh habitats of the flooded savanna. The newly flooded savanna acts as a prime nursery area for young fish since the flooded herbaceous vegetation provides protection from predation and produces an abundant supply of invertebrates that are utilized for food. The 114 stomachs of small juvenile piranhas contained mostly microcrustaceans and aquatic insects (Table 5-10). As size increased within this group there was a gradual switch from microcrustaceans to small aquatic insects. Primary food items, in order of importance (high $\%V_a$ and %D), were: cladocerans, chironomid larvae, copepods, and ostracods.

Comparison of Diets

Fish (flesh, fins, scales and small whole fish) were the main component of diets of all seven species of piranhas, both in terms of dominance and adjusted volume (Fig. 5-3). Only in small juveniles of Group I and juvenile *P. caribe* less than about 80 mm SL (or where sample sizes were small, e.g., Group IV *P. striolatus*) did non-fish items make up a large proportion. Most juveniles had eaten fish fins. Major exceptions were *P. caribe*, a generalist, and *C. mento*, a highly specialized scale-eater. Fins were usually from fishes similar in size to the predator. Based on this observation, one may assume juvenile piranhas were attacking small species or juveniles of other fishes. Whereas fish were the predominant food resource used by savanna populations, other vertebrates (i.e., mammals, birds, reptiles, and amphibians) were only of minor importance (Table 5-2).

Table 5-10. Food items of small juvenile piranhas (Size Class I, 10-19 mm SL), tentatively identified as *Pygocentrus caribe*, from the Apure River drainage (Caño Caicara area). %O=percent frequency of occurrence (nonempty stomachs); N = mean number per nonempty gut; %D = percent dominance; and $\%V_a$ = percent adjusted volume.

Number examined		114		
Number empty		3		
Food items	%O	N	%D	$\%V_a$
Plant material	5.4	nd[a]	-	-
Microcrustaceans	91.0	27.5	54.8	58.1
Aquatic insects	73.0	3.4	37.9	36.9
Other invertebrates	12.6	0.2	4.0	2.3
Other	7.2	nd[a]	3.2	2.7

[a] Not determined/not applicable

I rarely found evidence of seed-eating by piranhas in the Caño Caicara site, with the few seeds eaten being very small and probably taken incidentally along with intended prey items. Although other plant material, such as bits of leaves, grass blades, root wads, tiny flowers, and filamentous algae, was ingested, these items were usually of minor importance in terms of dominance and volume. Of hundreds of specimens examined, not one stomach contained many seeds. Most of the low Llanos, including gallery forests, do not produce many large fruits or big seeds. By way of comparison, stomachs of the herbivorous adults of *Mylossoma* sp. and *Metynnis* sp., taken in the Caño Caicara study area, were typically full of filamentous algae, masticated small seeds, and nonwoody vascular plant debris.

Diets and diet breadth usually changed with age. Diet breadth values were typically higher for the larger size classes (Fig. 5-3 and 5-4), but *C. mento* (the highly specialized scale-eater) had low diet breadth values (1.08 to 1.69) for all size groups. Group III *P. caribe*, with 5.92, had the widest breadth.

Table 5-11 is a matrix showing the diet overlap values for piranhas, by size class, from the Caño Caicara area. Cluster analysis of the Table 5-11 data produced four major trophic groupings (Fig. 5-5). Cluster I consisted of small juvenile piranhas that fed on small invertebrates, mostly microcrustaceans and aquatic insects. Cluster II contained seven species and three different size classes grouped together based on their high degree of piscivory. These piranhas frequently fed by cutting out chunks of flesh from other fish; however, diets also included an assortment of small fish taken whole, fish fins, and fish scales. Cluster III represented fin-eating piranhas. It included six species, and most were in size classes that included individuals between 20 and 80 mm SL. The only exception was adult *Serrasalmus elongatus* in the ≥160 mm SL size range. Cluster IV was composed of scale-eaters and represented by the three size classes of *Catoprion mento*. As a reflection of the intraspecific changes or shift in diet with age or size, most species were divided among two or more of the different cluster groupings.

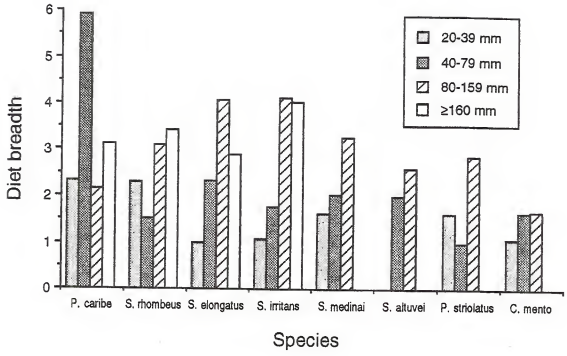


Fig. 5-4. Diet breadths estimated for eight piranha species, by size class, from the Caño Caicara area of the low Llanos, Apure River drainage, Orinoco River basin, Venezuela. Diet breadth calculated using formula of Levins (1968). Most species not represented in all size classes. Size ranges are standard length.

Table 5-11. Matrix of diet overlaps among different size classes of piranhas from Caño Caicara area, Apure River drainage, low Llanos. Overlap index is that of Schoener (1970); SL = Standard Length; JV = small juveniles; see Table 3-1 for species abbreviations.

Species and Size Range (mm SL)	PC 20-39	PC 40-79	PC 80-159	PC ≥160	SR 20-39	SR 40-79	SR 80-159	SR ≥160	SBL 20-39	SBL 40-79	SBL 80-159	SBL ≥160	SIR 20-39	SIR 40-79	SIR 80-159	SMD 20-39	SMD 40-79	SMD 80-159	PST 20-39	PST 40-79	PST 80-159	CM 20-39	CM 40-79	CM 80-159	SA 40-79	SA 80-159	JV 10-19
PC 20-39	100	35.2	5.75	10.7	43.6	2.1	11.2	4.5	0	1.05	10.05	1.05	2.4	3.3	6	14.25	4.85	3.3	14.35	0	13.3	2.5	3.25	1.05	1.05	1	62.9
PC 40-79		100	38.25	49.2	21.35	16.2	54.8	33.4	4.05	21.45	46.55	30.85	6.8	29.6	41.6	26.65	27.25	38.8	27.35	4.05	45	5.3	22.95	25.25	5.85	31.1	22.25
PC 80-159			100	56.05	0.3	20.25	24.45	47.35	0.3	18.7	61.3	28.1	3.05	28.05	66.25	11.9	25.3	68.95	10.3	0.3	28.1	5.55	16	8.2	24.4	53.05	2.5
PC ≥160				100	4.85	21	30.8	67	1.85	19.45	44.55	24.35	4.6	29.1	51.8	17.75	27.45	43.9	14.85	1.85	25.5	5.6	19.15	10.85	70.55	24.3	7.75
SR 20-39					100	56.45	45.45	31.55	56.5	56.5	18.2	37.5	56.45	56.45	21.25	66.2	56.5	20.15	69.8	56.5	0	0	0.8	0	0	31.25	43.5
SR 40-79						100	54	48.7	79.95	69.25	38.25	48.95	79.9	86.1	41.3	83.85	83.85	40.2	85.25	79.95	8.5	2.9	11.15	2.85	58.55	42.7	0
SR 80-159							100	39.2	0	15.55	54.45	24.95	46.8	63.6	60.2	18.75	19.55	62.1	19.05	0	42.8	2.1	23.55	27.25	18.15	45.4	2.25
SR ≥160								100	31.55	47.15	50.65	52.65	32.9	57.7	64.4	41.25	50.35	54.9	41.55	31.55	21	0	8.25	0	68.45	52.3	2.7
SBL 20-39									100	57.8	18.2	37.5	97.25	72.25	21.25	77.4	68.4	20.1	[illegible].7	100	0	0	0.8	0	50	31.3	0
SBL 40-79										100	52	79.7	57.75	74.65	51.05	64.3	79.8	48.05	[illegible]s	57.8	15.55	26.65	29.9	26.6	50	65.65	0
SBL 80-159											100	64.8	20.95	20.95	85.75	30.2	49.7	85.75	28.2	18.2	47.65	21.75	31	22.7	27.3	77.25	4.6
SBL ≥160												100	37.45	59.75	60.45	44	59.5	57.45	47.5	37.5	24.95	37.5	40.8	37.5	37.5	75.05	0
SIR 20-39													100	73.4	24	80.15	70.55	21.5	76.65	97.25	0	1.4	2.15	1.35	49.95	31.2	1.4
SIR 40-79														100	48.7	79.95	88.75	46.7	82.27	72.3	21.2	1.3	8.55	1.25	53.95	53.5	1.15
SIR 80-159															100	34.15	50.05	86.1	31.25	21.3	37.4	16.7	27.45	19.15	40.05	72.5	3.05
SMD 20-39																100	77.3	29.55	92.9	77.4	6.45	2.15	6.5	3.2	50	37.75	12.4
SMD 40-79																	100	50.15	78.4	68.4	17.15	10.45	16.9	9.6	54	53.25	1.6
SMD 80-159																		100	30.15	20.1	45.8	14.5	23.55	15.25	33.85	80.4	0.05
PST 20-39																			100	76.7	9.95	0	3.3	0	50	41.25	13.3
PST 40-79																				100	0	0	0.8	0	50	31.3	0
PST 80-159																					100	1.4	2.45	0	0	42.8	2.25
CM 20-39																						100	77.75	73.55	0	18.8	1.4
CM 40-79																							100	87.5	5.8	22.05	0
CM 80-159																								100	0	18.75	0
SA 40-79																									100	31.25	0
SA 80-159																										100	0
JV 10-19																											100

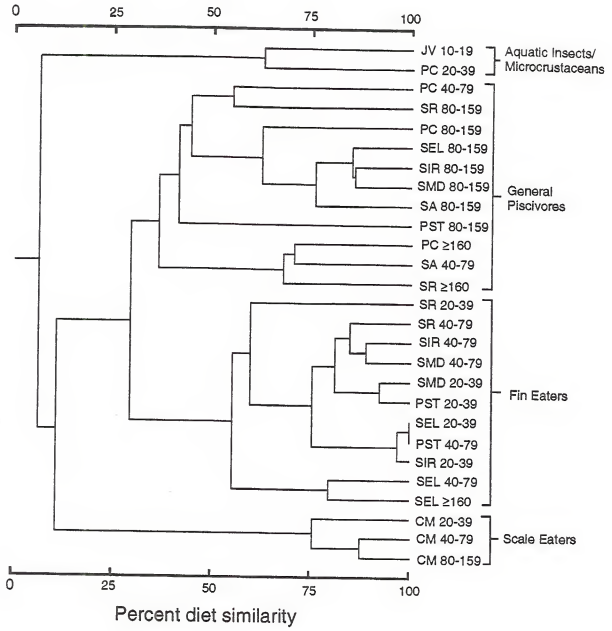


Fig. 5-5. Dendrogram from cluster analysis depicting similarities among diets of piranhas and related species (by size class) from the Caño Caicara area of the low Llanos, Apure River drainage, Orinoco River basin, Venezuela. Similarity values are from Table 5-11, dendrogram UPGMA-generated using overlap index of Schoener (1970). Size ranges are in mm Standard Length. Species abbreviations are as follows: PC = *Pygocentrus caribe*; PST = *Pristobrycon striolatus*; SMD = *Serrasalmus medinai*; SR = *Serrasalmus rhombeus*, SA = *Serrasalmus altuvei*, SIR = *Serrasalmus irritans*, SEL = *Serrasalmus elongatus*, and CM = *Catoprion mento*; JV = small juveniles.

CHAPTER 6
TROPHIC ECOLOGY OF PIRANHAS FROM THE UPPER ORINOCO

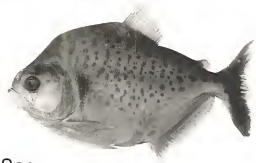
This chapter focuses on the trophic ecology of piranhas and related species from the upper Orinoco River basin of southern Venezuela, a region characterized by extensive lowland forests that undergo seasonal flooding. I also provide information on the diets of a few savanna populations not reported in the previous chapter, and compare feeding patterns of serrasalmine fishes from savanna with those from forested regions. Finally, I examine the relationship between intestine length and serrasalmine diets.

There have been few studies of the fishes inhabiting the upper Orinoco River region. To date, published works have dealt mainly with descriptions of new species or reports of species distributions as part of broader investigations on South American fish zoogeography. The research presented here is the first field study of fishes from the southern region of Venezuela aimed at understanding fish feeding patterns. Although feeding behaviors among certain piranha species are somewhat similar, the diets of several species have not been reported previously. The eight species of piranhas examined from the upper Orinoco are *Serrasalmus rhombeus*, *S. manueli*, *S. cf. eigenmanni*, *S. altuvei*, *Pygocentrus caribe*, *Pygopristis denticulatus*, *Pristobrycon striolatus*, and an undescribed *Pristobrycon* sp. (Fig. 6-1). I also report on the diets of several other serrasalmine fishes, focusing primarily on *Catoprion mento*, *Myleus asterias*, *M. schomburgkii*, and *M. torquatus*.

Fig. 6-1. Eight piranha species from the upper Orinoco River basin of Venezuela. Sm = *Serrasalmus manueli*, Sr = *S. rhombeus*, Seg = *S.* cf. *eigenmanni*, Sa = *S. altuvei*, Pst = *Pristobrycon striolatus*, Pc = *Pygocentrus caribe*, Pyp = *Pygopristis denticulatus*, and Psp = *Pristobrycon* sp.

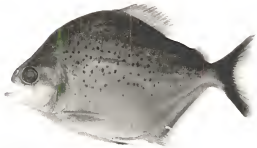
Sm

Sr

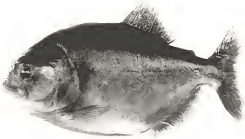


Seg

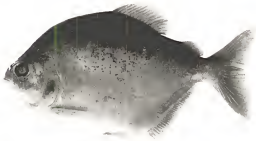
Sa



Pst



Pc



Pyp

Psp

Species Accounts

Figure 6-2 is a summary of the diets by size class of the eight piranha species taken in the upper Orinoco. A partial listing of prey items identified from the stomachs of the common piranhas is given in Table 6-1. In this section I describe the general morphology, local distribution and habitat, as well as the diets for each of the upper Orinoco piranhas and several other serrasalmine fishes.

Serrasalmus rhombeus (Linnaeus 1766)

Serrasalmus rhombeus was the most abundant piranha in most samples from the upper Orinoco River. Greatest numbers were found in whitewaters such as the Ocamo and Paru rivers where they typically inhabited main channel borders. *Serrasalmus rhombeus* (Fig. 6-1) was also the largest piranha species taken, reaching well over 350 mm SL. Like many piranhas, it varies ontogenetically in both body form and coloration. Juveniles have a moderately elongate body and pointed snout, whereas adults are robust with a relatively deep body. Juvenile body color is silver with black spotting, and the caudal fin has a terminal black band. The body and fins of large adults are darkly pigmented, typically gray or blue black.

Serrasalmus rhombeus was one of the most carnivorous of the upper Orinoco piranhas (Fig. 6-2 and Table 6-2). Individuals from 40-159 mm SL (Groups III-IV) fed mostly on fish flesh and fins, and the largest specimens examined (≥160 mm) had fed mainly on small fish. Only a few of the prey fish ingested could be identified (Table 6-1). A large *S. rhombeus* contained the skeletal remains of an adult toad identified as *Bufo marinus*, but overall they rarely preyed upon non-fish vertebrates. Plant material was also relatively unimportant in their diet, small quantities being found in stomachs of only 11 of the 83 specimens and accounting for less than 5% of the total food volume. Most or all of these plant items were probably ingested incidentally while attacking other prey. Plant

Fig. 6-2. Diets by size class (≥ 40 mm SL) of eight piranha species from the upper Orinoco River basin, Venezuela. Size of segments represents percentage of volume (%V) of each prey type; n = number of stomachs examined; numbers in parentheses represent diet breadth using formula of Levins (1968).

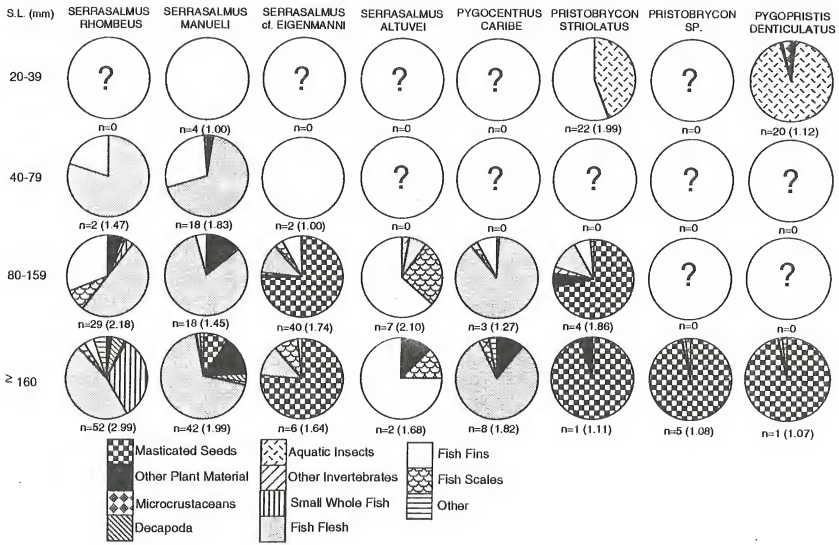

S.L. (mm)
SERRASALMUS RHOMBEUS
SERRASALMUS MANUELI
SERRASALMUS cf. EIGENMANNI
SERRASALMUS ALTUVEI
PYGOCENTRUS CARIBE
PRISTOBRYCON STRIOLATUS
PRISTOBRYCON SP.
PYGOPRISTIS DENTICULATUS
20-39
40-79
80-159
≥ 160
n=0
n=4 (1.00)
n=0
n=0
n=0
n=22 (1.99)
n=0
n=20 (1.12)
n=2 (1.47)
n=18 (1.83)
n=2 (1.00)
n=0
n=0
n=0
n=0
n=0
n=29 (2.18)
n=18 (1.45)
n=40 (1.74)
n=7 (2.10)
n=3 (1.27)
n=4 (1.86)
n=0
n=0
n=52 (2.99)
n=42 (1.99)
n=6 (1.64)
n=2 (1.68)
n=8 (1.82)
n=1 (1.11)
n=5 (1.08)
n=1 (1.07)
Masticated Seeds
Other Plant Material
Microcrustaceans
Decapoda
Aquatic Insects
Other Invertebrates
Small Whole Fish
Fish Flesh
Fish Fins
Fish Scales
Other

Table 6-1. List of taxa identified from the stomach contents of the three most common piranha species from upper Orinoco River drainages, Venezuela.

Species	Food Item (frequency of occurrence)
Serrasalmus rhombeus	Fish remains (small whole fish or flesh): Ctenoluciidae - *Boulengerella* sp. (1); catfish: Callichthyidae - *Corydoras* sp. (1); Auchenipteridae (1); Pimelodidae (1); Doradidae (probably *Liphodoras*).(1); unidentified catfish remains (2); Cichlidae (2), other fish (32).
	Bird: fragments of feather and bone (1).
	Amphibians: skeletal remains of adult toad *Bufo marinus*.(1).
	Invertebrates: Decapoda: crab (1); Arthropoda - terrestrial beetle (1), adult beetle Gyrinidae (1), insect larva (1), unidentified insect (1), terrestrial insect (1), Orthopteran leg (1); Gastropoda - snail (1).
	Plant Material: Filamentous algae (1); unidentified flower (1); leaf or leaf fragments (2); woody twigs (1); root fibers (5), seed fragments? (2)
Serrasalmus manueli	Fish (whole fish or flesh): characoid ( ); Cichlidae - juvenile *Cichla temensis*.(1): gymnotoid eel remains (1); catfish remains (Doradidae or Auchenipteridae) (2), catfish remains (1), unidentified fish (24).
	Reptiles: Lizard remains (1).
	Invertebrates: Decapoda: *Macrobrachium olfersi* (1), unidentified shrimp (2), decopod leg fragment (1); terrestrial insect (3), unidentified insect (1).
	Plant Material: small flowers of a Lecythidaceae - *Gustavia* sp.? (1); Palmae - fruit of *Bactris gasipaes* ? (2); unidentified masticated seeds (9); leaf fragments (3); unidentified pieces of fruit (exocarp and mesocarp) (1); vascular plant material (2).
Serrasalmus cf. eigenmannii	Fish (whole fish or flesh): unidentified fish remains (7).
	Plant Material (all unidentified): flowers fregments (2); masticated seeds (mostly endocarp) (35).

Table 6-2. Food items of *Serrasalmus rhombeus* from the upper Orinoco River basin by size class. %O = percent frequency of occurrence; %D = percent dominance; and %V = percent volume. N = 83.

Size class (mm, SL)	III (40-79)			IV (80-159)			V (≥160)		
Number examined	2			29			52		
Number empty	0			7			16		
Food items	%O	%D	%V	%O	%D	%V	%O	%D	%V
Plant material	-	-	-	18.2	4.6	5.1	13.9	5.3	1.9
Decapoda	-	-	-	-	-	-	2.8	2.6	5.2
Aquatic insects	-	-	-	4.6	4.6	0.7	-	-	-
Other invertebrates	-	-	-	13.6	-	1.5	5.6	2.6	0.7
Small whole fish				4.6	4.6	3.4	8.3	5.3	33.3
Fish flesh	50.0	50.0	80.0	40.9	36.4	49.8	58.3	50.0	46.3
Fish fins	50.0	50.0	20.0	59.1	40.9	31.0	13.9	13.2	3.8
Fish scales	-	-	-	22.7	9.1	8.6	25.0	15.8	3.0
Other	-	-	-	-	-	-	8.3	5.3	5.9

materials eaten by four Group IV fish consisted of a small leaf, fine roots, and a small amount of filamentous algae, while five large adults (≥160 mm SL) had fed on an unidentified flower, a leaf fragment, woody twigs, and some small root fibers.

My samples of *Serrasalmus rhombeus* from the upper Orinoco did not include individuals less than 40 mm SL. Juveniles found in the low Llanos frequently take fins, as is probably true also for young *S. rhombeus* inhabiting the upper Orinoco. IL/SL ranged from 0.9 for a 158-mm SL fish, to a high of 1.7 for a 233-mm SL adult.

Serrasalmus manueli Fernandez-Yepez and Ramirez 1967

Serrasalmus manueli was the most abundant piranha in many of the blackwater rivers, such as the Atabapo and the Sipapo. It was also found together with *S. rhombeus* in a few of the larger whitewater rivers, including the upper Orinoco main stem and the Ventuari. *Serrasalmus manueli* (Fig. 6-1) was the second largest piranha found in the upper Orinoco basin; individuals over 270 mm SL were fairly common, and one specimen from the Atabapo drainage was 340 mm SL. The shape of the body is similar to *S. rhombeus*. Young are relatively elongate and sharp-snouted, whereas large adults have a fairly deep, thick body, and broad, powerful jaws. The body of *S. manueli* has many elongated vertical and irregularly-shaped dark markings, and black coloring is found along the base of the caudal fin. Large juveniles and adults have a large, black humeral spot, and the cheek and breast of adults are sometimes red-orange. The body color of *S. manueli* changes from silvery to almost black with age as is true also for *S. rhombeus*. However, like many neotropical fish, those inhabiting blackwaters are darker or more heavily pigmented than individuals taken in turbid whitewaters. Unique among piranhas, the first few anterior rays of the dorsal fin have filaments that may be greatly elongated in older juveniles and adults, but most individuals lose this ornamentation to other fin-eating fishes.

The diet of *Serrasalmus manueli* has never before been reported. Diets of specimens from the upper Orinoco are given in Figures 6-2 and Table 6-3. Large *S.*

manueli (≥160 mm SL) preyed heavily on fishes, but plant material was occasionally taken in mass, with plant matter occurring in 12 of 42 Group V stomachs and accounting for 25% of total food volume. Five of six adult *S. manueli* (≥160 mm SL), caught with hook and line in the Sipapo River during high water, contained large amounts of masticated seeds, primarily endocarp, and the sixth was packed with small flowers of a Lecythidaceae, possibly *Gustavia* sp. Seven specimens from other forest sites had fed on leaf fragments and pieces of fruit (exocarp and mesocarp); some of the fruit was identified as the palm *Bactris gasipaes* (Palmae). Prey fishes and other items identified from stomachs are given in Table 6-1. IL/SL ranged from 0.7 for a 52-mm SL juvenile, to 2.2 for a 250-mm SL adult.

In addition to the 78 large specimens, I examined five small *Serrasalmus* (<40 mm SL) that I tentatively identified as juveniles of *S. manueli*. These small fish, together with young of *Pristobrycon striolatus*, were taken from a clump of macrophytes near the banks of the lower Yureba River, a blackwater tributary of the Ventuari. All five fish had a prominent black spot on the dorsal fin and well-developed ectopterygoid teeth. The stomach of a single individual less than 20 mm SL (Group I) contained aquatic insects (Fig. 6-3), while those of four Group II individuals were packed with fins of other small fishes (Fig. 6-3, Table 6-3). IL/SL of these small juveniles was less than 1.0.

Serrasalmus cf. *eigenmanni* Norman 1928

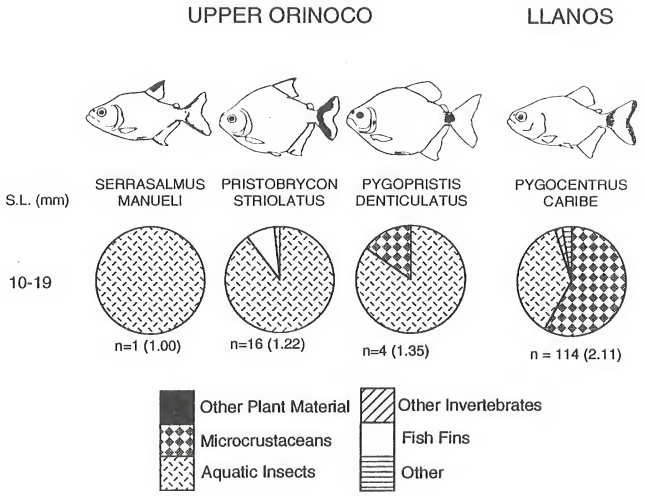
Serrasalmus cf. *eigenmanni* was the third most common piranha in samples from the upper Orinoco. It was the most abundant piranha taken in the Mavaca River drainage, was relatively common in the Ocamo and Matacuni drainages, and a single individual was taken from the Paru River of the lower Ventuari. All of the above are basically whitewater rivers. *Serrasalmus* cf. *eigenmanni* (Fig. 6-1) is a medium-sized piranha, the largest specimens collected being two gravid females of 180 mm SL. It has a somewhat blunt snout, and in terms of body shape, most resembles *S. medinai*, a species found in the

Table 6-3. Food items of *Serrasalmus manueli* from the upper Orinoco River basin by size class. %O = percent frequency of occurrence; %D = percent dominance; and %V = percent volume. N = 82.

Size class (mm, SL)	II (20-39)			III (40-79)			IV (80-159)			V (≥160)		
Number examined	4			18			18			42		
Number empty	0			5			7			16		
Food items	%O	%D	%V	%O	%D	%V	%O	%D	%V	%O	%D	%V
Masticated seeds	-	-	-	-	-	-	9.1	-	0.1	30.8	19.2	9.5
Plant material	-	-	-	15.4	7.7	1.5	27.3	18.2	13.1	15.4	11.5	15.1
Decapoda	-	-	-	-	-	-	-	-	-	15.4	3.8	2.9
Aquatic insects	-	-	-	-	-	-	9.1	-	0.01	-	-	-
Other invertebrates	-	-	-	7.7	-	0.8	18.2	18.2	1.0	11.5	7.7	1.2
Fish flesh	-	-	-	38.5	30.8	68.2	45.5	40.9	81.8	69.2	46.2	68.5
Fish fins	100.0	100.0	100.0	28.7	57.7	28.7	27.3	22.7	4.1	3.8	3.8	1.4
Fish scales	-	-	-	7.7	-	0.1	-	-	-	11.5	-	0.3
Other	-	-	-	7.7	3.8	0.8	-	-	-	11.5	7.7	1.0

Note: Stomach contents of a single specimen of Group I size class (10-19 mm SL) consisted of aquatic insects.

Fig. 6-3. Diets of selected small juvenile piranhas (10-19 mm SL) from upper Orinoco River drainages and the low Llanos, Venezuela. Size of segments represents percentage of volume of each prey type; n = number of stomachs examined; numbers in parentheses represent diet breadth using formula of Levins (1968).


UPPER ORINOCO
LLANOS
S.L. (mm)
SERRASALMUS MANUELI
PRISTOBRYCON STRIOLATUS
PYGOPRISTIS DENTICULATUS
PYGOCENTRUS CARIBE
10-19
n=1 (1.00)
n=16 (1.22)
n=4 (1.35)
n = 114 (2.11)
Other Plant Material
Microcrustaceans
Aquatic Insects
Other Invertebrates
Fish Fins
Other

Llanos. Individuals of all sizes are silver-colored and have numerous irregularly-shaped dark spots, with the number and shape of the spots being quite variable. Adults have a rather faint black humeral spot. The base of the caudal fin is black, which in older fish covers nearly the entire tail except for a terminal hyaline band. Parts of the cheek and breast, as well as the pectoral and anal fins, are reddish orange. Although *Serrasalmus* cf *eigenmanni* may involve a species complex (W. Fink, personal communication), I distinguished only one species in my samples.

The diet of this species has not been reported previously. All larger *S.* cf. *eigenmanni* were primarily seed predators (Fig. 6-2 and Table 6-4). Masticated seeds, mostly endocarp, were found in 35 of 46 Group IV and V specimens and accounted for 75% of total food volume. The only other plant materials found were fragments of mature flowers in two stomachs. Unfortunately none of the seeds or flowers could be identified. Although its natural diet consisted primarily of seeds, as in other piranhas, adult *S.* cf. *eigenmanni* readily take hooks baited with fish flesh. The stomachs of two young juveniles (48 and 76 mm SL) examined were packed exclusively with fins of other small fishes. IL/SL ratio (n = 32) ranged from 0.9 for a 48-mm SL juvenile, to 3.4 for a 129-mm SL adult.

Serrasalmus altuvei Ramirez 1965

Serrasalmus altuvei was uncommon in samples from the upper Orinoco. It is a medium-sized piranha, with a slender pointed snout and a deep body that is more laterally compressed than that of most other piranhas (Fig. 6-1). The body is silvery, and the sides are covered with black spots that are vertically elongated in most juveniles and some adults. Large juveniles and adults have a dark humeral spot and a black terminal band on the caudal fin. Live *S. altuvei* from the Mavaca River were found to have a partly red iris, which was less intense than that of *S. rhombeus*. I collected 12 fish (119-169 mm SL), from the Mavaca, Ocamo and Matacuni rivers, and examined the stomach contents of 9 specimens

Table 6-4. Food items of *Serrasalmus* cf. *eigenmanni* from the upper Orinoco River basin by size class. %O = percent frequency of occurrence; %D = percent dominance; and %V = percent volume. N =4 8.

Size class (mm, SL)	III (40-79)			IV (80-159)			V (≥160)		
Number examined	2			40			6		
Number empty	0			2			0		
Food items	%O	%D	%V	%O	%D	%V	%O	%D	%V
Masticated seeds	-	-	-	78.9	63.2	74.4	83.3	83.3	76.4
Plant material	-	-	-	5.3	-	0.9	-	-	-
Aquatic insects	-	-	-	2.6	-	0.4	-	-	-
Other invertebrates	-	-	-	7.9	2.6	1.1	-	-	-
Fish flesh	-	-	-	15.8	13.2	11.6	33.3	-	12.4
Fish fins	100.0	100.0	100.0	39.5	18.4	7.6	16.7	-	1.6
Fish scales	-	-	-	26.3	-	3.6	33.3	16.7	9.5
Other	-	-	-	2.6	-	0.4	-	-	-

(Table 6-5 and Fig. 6-2). Fins were the most important food item, accounting for 63.9% of total food volume; scales were second in importance, 25.9% by volume. IL/SL ratio (n = 8) ranged from 0.65 to 1.02 (mean = 0.87).

Pygocentrus caribe (Lutken 1874)

Although it was the most abundant piranha in many fish communities in the low Llanos, *Pygocentrus caribe* was uncommon in samples from the upper Orinoco, and was restricted to more lentic habitats such as abandoned river meanders and floodplain lakes. *Pygocentrus caribe* (Fig. 6-1) is a robust, heavy-bodied species with broad and powerful jaws; individuals reach about 300 mm SL. The body is silvery, and the cheek and venter are often bright reddish orange, usually with a prominent black humeral spot. Based on observations of *P. caribe* collected in other parts of Venezuela, the body and fins of large adults in breeding condition turn almost black.

My samples showed that *Pygocentrus caribe* is primarily a piscivore. Examination of stomach contents of 11 specimens (135-235 mm SL) from the upper Orinoco (Fig. 6-2) indicated that fish flesh was the main prey in terms of frequency of occurrence, volume, and dominance. Food items were as follows (%O-%D-%V): Group IV (n=3)-other invertebrates (66.7-0-0.7), fish flesh (100.0-100.0-88.4), fish fins (66.7-0-8.3), fish scales (66.7-0-2.7); Group V (n=8, 3 empty)-plant material (80.0-40.0-9.4), fish flesh (80.0-60.0-71.8), fish fins (20.0-0-0.7), fish scales (20.0-0-15.5), other (20.0-0-2.7). Plant material consisted of leaf fragments and woody material, which most likely was taken incidental to attacking or ingesting other prey. No small juveniles of *P. caribe* were found in the upper Orinoco. IL/SL was low, ranging from 0.7 to 1.4 for the 11 specimens examined.

Table 6-5. Food items of *Serrasalmus altuvei* from drainages of the upper Orinoco River basin, by size class. %O = percent frequency of occurrence; %D = percent dominance; and %V = percent volume. N = 9.

Size class (mm, SL)	IV (80-159)			V (≥160)		
Number examined	7			2		
Number empty	1			1		
Food items	%O	%D	%V	%O	%D	%V
Plant material	-	-	-	100.0	-	12.5
Aquatic insets	33.3	-	2.5	-	-	-
Other invertebrates	16.7	-	0.2	-	-	-
Fish flesh	50.0	33.3	7.0	-	-	-
Fish fins	66.7	50.0	63.1	100.0	100.0	75.0
Fish scales	66.7	16.7	27.0	100.0	-	12.5
Other	16.7	-	0.2	-	-	-

Pristobrycon striolatus (Steindachner 1908)

Pristobrycon striolatus was rare in my samples from the upper Orinoco. It is a medium-sized piranha found in both the Llanos and in southern Venezuela. The body is silvery, partly covered with very small black spots, and has black along the base of the caudal fin. The cheek and breast are typically reddish orange. My upper Orinoco sample consisted of five adult specimens (106-165 mm SL), all taken during low water, four from Caño Jenita of the Ocamo River, and one from a lagoon of the Mavaca River. The stomachs of all five adults were packed with unidentifiable crushed seeds (Fig. 6-2 and Table 6-6), which accounted for 84% of total food volume. Other plant material included small stems and flower fragments. IL/SL ratio of the five specimens ranged from 1.5 to 2.8.

In addition to the larger fish, I also examined 38 small *Pristobrycon* juveniles (<40 mm SL), tentatively identified as *P. striolatus*. Characteristic of the genus, they had a preanal spine (Fink, personal communication), but lacked ectopterygoid teeth. All were taken from a mat of aquatic vegetation near the shore of the Yureba River, a blackwater tributary of the Ventuari. Those of 10 to 19 mm SL fed heavily on the larvae of aquatic insects (7.2 insects per stomach), mostly small chironomids, trichopterans and ephemeropterans (Fig. 6-3). Food items of these Group I *P. striolatus* (n = 16) were as follows (%O-%D-%V): microcrustaceans (18.8-0-1.7), aquatic insects (93.8-93.8-90.0), and fish fins (12.5-6.3-8.3). Stomachs of fish 20-39 mm SL (n = 22, 2 empty) had fed mostly on fins (55.3% by volume) and aquatic insects (44.3%) (Fig. 6-2). Aquatic insects (3.1 per stomach) identified from stomachs comprised chironomids, ephemeropterans, and coleopteran larvae and pupae. Mean IL/SL for small juveniles was less than 1.0.

Pristobrycon sp.

Pristobrycon sp. is a rare species. My sample consisted of only five adult fish (182-245 mm SL) all taken in November during high water from flooded forest along Caño

Table 6-6. Food items of *Pristobrycon striolatus* from the upper Orinoco River basin by size class. %O = percent frequency of occurrence; %D = percent dominance; and %V = percent volume. N = 43.

Size class (mm, SL)	I (19-20)			II (20-39)			IV (80-159)			V (≥160)		
Number examined	16			22			4			1		
Number empty	0			2			0			0		
Food items	%O	%D	%V	%O	%D	%V	%O	%D	%V	%O	%D	%V
Masticated seeds	-	-	-	-	-	-	75.0	60.0	71.8	100.0	100.0	95.0
Plant material	-	-	-	-	-	-	50.0	20.0	5.7	100.0	-	4.5
Microcrustaceans	18.8	-	1.7	-	-	-	-	-	-	-	-	-
Aquatic insects	93.8	93.8	90.0	50.0	50.0	44.3	-	-	-	-	-	-
Other invertebrates	-	-	-	5.0	-	0.4	25.0	-	2.9	-	-	-
Fish flesh	-	-	-	-	-	-	25.0	20.0	12.0	-	-	-
Fish fins	12.5	6.3	8.3	50.0	50.0	55.3	50.0	-	6.7	-	-	-
Fish scales	-	-	-	-	-	-	-	-	-	100.0	-	0.5
Other	-	-	-	-	-	-	25.0	-	1.0	-	-	-

Chimita, Atacavi River, with gill net and handlines. The only other specimen known is that of a single fish taken from a tributary of the blackwater Pasimoni River in the upper Rio Negro drainage of Venezuela (W. Fink, personal communication). The species is currently being described as new by W. Fink and A. Machado-Allison, and the five fish reported on here will be part of the type series. *Pristobrycon* sp. is a medium to large-sized piranha with a rounded snout and a fairly robust body that is covered with irregularly-shaped black markings (Fig. 6-1). It is known locally as "*caribe colorado*" (a name sometimes applied to *Pygocentrus caribe*) because of the bright red-orange color that marks most of the lower body and the lower fins. Intensity of body coloration is probably related to breeding condition. Three of the specimens were females, of which one had the gonads almost completely developed indicating that spawning takes place near the end of the rainy season. Curipaco Indians collect adults in the flooded forest by pole fishing using small hooks baited with earthworms; they maintain that the young of *Pristobrycon* sp. move from the flooded forests into streams during low water where they are easily caught with nets or killed with fish poisons derived from plants (*barbasco*).

Pristobrycon sp. is a seed predator (Fig. 6-2); stomachs of all five specimens were packed with unidentified crushed seeds, mostly endocarp plus some exocarp and mesocarp. Food items were as follows (%O-%D-%V; all Group V): masticated seeds (100.0-100.0-96.4), plant material (leaf fragment of a palm) (20.0-0-0.4), other invertebrates (winged insects and fragments of a spider) (60.0-0-1.4), and fish scales (20-0-1.8). Intestines were very long for piranhas, ranging from 630 to 800 mm; IL/SL ranged from 2.7 to 4 for the five specimens examined.

Pygopristis denticulatus Muller and Troschel 1845

Pygopristis denticulatus (Fig. 6-1) was uncommon in my samples. I collected only one adult (175 mm SL) from the upper Orinoco, taken from Caño Cuchakén of the blackwater Atabapo River. I also preserved 80 small juvenile *P. denticulatus* (15-37 mm

SL) taken from a shallow, blackwater oxbow lake covering several hectares in the forested floodplain of the Mavaca River; several additional fish were transported alive for later observation. The species is the only representative of the genus *Pygopristis*, and closely resembles *Pristobrycon striolatus* in both body form and markings. *Pygopristis denticulatus* is the only piranha with five cusps (pentacuspid) on the jaw teeth, whereas adults of all other piranhas have only three (tricuspid) (Machado-Allison 1985). The body is deep, the snout is somewhat rounded, and the jaws are relatively small compared with that of *S. rhombeus*. The body is typically silvery and sometimes dark, and parts of the cheek and breast, as well as most fins, are red-orange. Juveniles are silvery, and parts of unpaired fins are reddish orange. From about 25 mm SL, the sides are marked by a series of about ten brownish, vertical bars, narrow and somewhat irregularly shaped; the bars become faint with age. Unpaired fins are marked with a thin, blue-white terminal border.

Results of stomach content analysis are given in Figure 6-2 and Table 6-7. The stomach of the single adult examined was full of masticated seeds (96.8% by volume) along with a few fish scales (1.6%) and the remains of two small invertebrate larvae (1.6%) (Fig. 6-2). IL/SL was 1.9. I examined the stomach contents of 24 of the 80 preserved juveniles (Table 6-7). Both Group I (Fig. 6-3) and II (Fig. 6-2) had fed heavily on aquatic insects, mostly chironomid and ephemeropteran larvae, and odonata nymphs. Upon reaching a SL of about 40 mm SL a single juvenile that had survived in an aquarium began stalking and chasing other fishes and clipping out pieces of fins.

Other Serrasalmine Fishes

In addition to piranhas, there are several other genera of the subfamily Serrasalminae that occur in the upper Orinoco basin. *Catoprion*, a monotypic genus, is a fin eater widely distributed in South America. All other genera of serrasalmine fishes, a group in dire need of taxonomic revision, are primarily herbivores and all have relatively

Table 6-7. Food items of *Pygopristis denticulatus* from the upper Orinoco River basin by size class. %O = percent frequency of occurrence; %D = percent dominance; and %V = percent volume. N = 25.

Size class (mm, SL)	I (10-19)			II (20-39)			V (≥160)		
Number examined	4			20			1		
Number empty	0			0			0		
Food items	%O	%D	%V	%O	%D	%V	%O	%D	%V
Masticated seeds	-	-	-	-	-	-	100.0	100.0	96.8
Plant material	-	-	-	20.0	-	1.7	-	-	-
Microcrustaceans	100.0	-	15.2	5.0	5.0	3.7	-	-	-
Aquatic insects	100.0	100.0	84.8	95.0	95.0	94.1	-	-	-
Other invertebrates	-	-	-	5.0	-	0.7	100.0	-	1.6
Fish scales	-	-	-	-	-	-	100.0	-	1.6
Other	-	-	-	5.0	-	<0.1	-	-	-

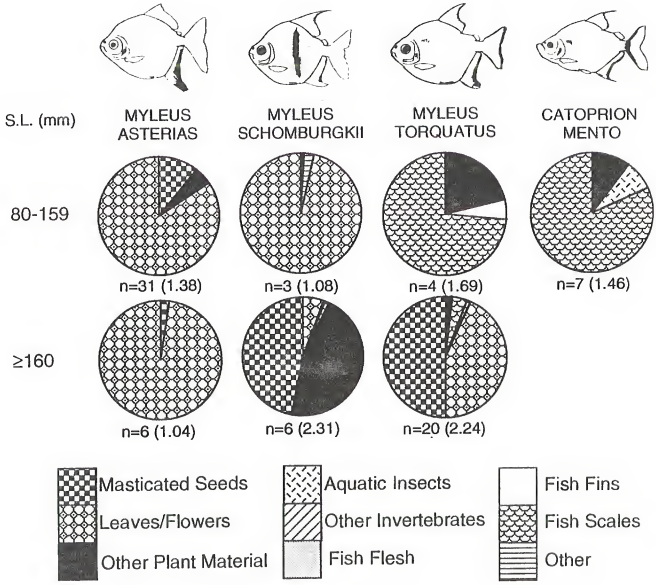
long intestines. The diets of several of the more commonly encountered species are presented in Figure 6-4.

Catoprion mento (Cuvier 1819) Although locally abundant in parts of the low Llanos, *C. mento* was uncommon in my samples from southern Venezuela, where it was limited to lentic, back-water areas. It is a small species; those taken in the upper Orinoco, all over 90 mm SL, were some of the largest I saw in all of Venezuela. The body is silvery, cheek usually marked with reddish orange. Both males and females may have long filaments extending from the first rays of dorsal fin. The seven large adults examined (99 to 128 mm SL) contained mostly fish scales (81.7% by volume) and a small amount of plant material (10.4%) (pieces of leaves, and some filamentous algae), and aquatic insects (8.0%) (Fig. 6-4). IL/SL ratio (n=7) ranged from 0.7 to 0.9.

Myleus species. The genus *Myleus* is represented by several species of deep-bodied, laterally compressed fishes. Jaw teeth are essentially molariform, with high cusps that are adapted for cutting and possibly crushing plant material. The sexes exhibit striking differences in body color and fin morphology; the males sometimes develop bright colors and long fin filaments that are most pronounced during the breeding season. Three species of *Myleus* were common in my samples from the upper Orinoco, *Myleus asteias, M. schomburgkii*, and *M. torquatus*.

Myleus asterias was the most common species of this genus encountered. My largest specimen was 185 mm SL, although maximum size may be much larger. It is a silvery fish, with the bodies of males often spotted with variable hues of purple and yellow. The anal fin of the male consists of two lobes with very small hooks present during the breeding season. In contrast, the anal fin of females forms single a long lobe. Most of the 37 specimens examined (98-185 mm SL) contained leaves that had been clipped or sliced into small fragments (Fig. 6-4). Food items were as follows (%O-%D-%V): Group IV (n=31, 2 empty)-masticated seeds (24.1-12.1-10.9), leaves/flowers

Fig. 6-4. Diets by size class (≥80 mm SL) of four serrasalmine species from the upper Orinoco River basin: *Catoprion mento*, *Myleus asterias*, *M. schomburgkii*, and *M. torquatus*. Size of segments represents percentage of volume of each prey type; n = number of stomachs examined; numbers in parentheses represent diet breadth using formula of Levins (1968).


S.L. (mm)
MYLEUS ASTERIAS
MYLEUS SCHOMBURGKII
MYLEUS TORQUATUS
CATOPRION MENTO
80-159
n=31 (1.38)
n=3 (1.08)
n=4 (1.69)
n=7 (1.46)
≥160
n=6 (1.04)
n=6 (2.31)
n=20 (2.24)
Masticated Seeds
Leaves/Flowers
Other Plant Material
Aquatic Insects
Other Invertebrates
Fish Flesh
Fish Fins
Fish Scales
Other

(93.1-74.1-84.4), other plant material (24.1-13.8-4.6), fish scales (3.4-0-0.1); Group V (n=6)-masticated seeds (16.7-0-2.2), leaves/flowers (100.0-100.0-97.8). Several of the flowers could be identified: one stomach was packed with small whole flowers of a *Machaerium* sp. (Papilionaceae), and a second contained flower fragments of a *Campsiandra* sp. (Caesalpiniaceae). Four fish collected in an abandoned meander of the Putaco River with dense aquatic vegetation had fed on flowers and leaves of the water lettuce *Pistia stratiotes* (Araceae).

Myleus torquatus was taken along the main channels of rivers and streams, but not in backwater areas. It is a medium-sized fish. The body coloration is silver, and there is a black border on the caudal fin that may vary widely in intensity. A few males had long dark filaments extending from the dorsal-fin rays. My examination of the stomachs of 24 individuals (109-192 mm SL) (Fig. 6-4) indicated that the species is highly opportunistic in its feeding behavior. Many stomachs contained either crushed seeds or well-digested fruit; one was full of cooked white rice (having fed on our discarded camp food); the stomachs of several specimens were packed with large scales. Because scales of serrasalmine fishes are small, scale eating was not the result of intraspecific aggression. Unlike other members of the genus examined, *Myleus torquatus* has a unique "overbite", the upper jaw extending past the lower jaw, causing several of the upper teeth to be exposed. Other scale-eating fish are known to ram their victims and use their projecting teeth to dislodge scales (Sazima and Machado 1982, Sazima 1983); the exposed teeth of *M. torquatus* could be used for the same purpose. Food items were as follows (%O-%D-%V): Group IV (n=4, 2 empty) - plant material (50.0-50.0-21.1), fish fins (50.0-0-5.3), fish scales (50.0-50.0-73.7); Group V (n=20, 2 empty) - masticated seeds (77.8-61.1-50.4), leaves/flowers (27.8-27.8-43.6), other plant material (5.6-5.6-1.0), other invertebrates (11.0-0-0.2), fish flesh (5.6-0-0.2), fish scales (22.2-0-3.9), and other (5.6-5.6-0.7). IL/SL ranged from 2.6 to 3.2.

Myleus schomburgkii. *M. schomburgkii*, possibly a species complex (Machado-Allison, personal communication), is fairly common and widespread in the upper Orinoco, and is also found in the Capanaparo and Cinaruco rivers of the Llanos. Maximum size is over 300 mm SL. *Myleus schomburgkii* is silvery, with a single large black marking that runs vertically on each side of the body that gives the appearance of having been stroked with a paint brush. In breeding males the dorsal fin develops many long black filaments, and large parts of the body may be covered with various combinations of bright reddish orange, dark red, and black. I examined the stomachs of nine specimens (87-310 mm SL) (Fig. 6-4). Common food items included seeds (masticated), filamentous algae, and fragments of leaves of a bryophyte. IL/SL ranged from 2.3 to 3.8. Seeds were also the most important food item in eight *M. schomburgkii* collected in the Llanos during the dry season.

Summary of Upper Orinoco Trophic Patterns

Table 6-8 presents a matrix giving the diet overlap values, calculated by size class for eight piranhas and four related species from the upper Orinoco River basin. Cluster analysis of the Table 6-8 data produced six major trophic groupings or feeding guilds (Fig. 6-5): general piscivore, aquatic insectivore, scale-eater, fin-eater, seed-predator, and folivore. Cluster I includes the general piscivores, predators that bit out chunks of flesh from other fishes or ate small fish whole; this guild consisted of three species in the three larger size classes (≥40 mm SL). Cluster II were fin eaters and consisted of four piranha species and four different size classes. Cluster III, the seed-predator guild, consisted of fish that fed mostly on seeds, which they bit into small fragments before ingesting. Seed-predators were represented by six species in the two larger size classes. Cluster IV were scale-eaters, represented by two species. Cluster IV were folivores, fish that fed on leaves and flowers, usually by clipping them into small fragments; this group was limited to two

Table 6-8. Matrix of diet overlaps among different size classes of serrasalmine fishes from upper Orinoco River drainages. Overlap index is that of Schoener (1970). (SL = Standard Length, see Table 3-1 for species abbreviations).

Species and Size Range (SL, mm)	SR 40-79	SR 80-159	SR ≥160	SM 40-79	SM 80-159	SM ≥160	SEG 40-79	SEG 80-159	SEG ≥160	PC 80-159	PC ≥160	PST 80-159	PST ≥160	PSP ≥160	PYP ≥160
SR 40-79	100	69.75	50.05	88.16	84.05	69.95	20	19.2	14.05	88.25	72.45	18.65	0	0	0
SR 80-159		100	59	80.79	59.91	57.8	31	25.15	22.6	61.4	64.1	25.2	4.95	3.55	3.05
SR ≥160			100	53.09	52.6	54.5	3.8	20.35	17	53.4	54.5	19.3	2.35	2.85	2.25
SM 40-79				100	74.51	72.79	28.7	21.34	14.09	77.19	71.19	21.71	1.54	1.24	0.84
SM 80-159					100	84.1	4.1	17.66	14.1	86.5	81.8	22.8	4.55	1.45	1.05
SM ≥160						100	1.4	25.25	23.7	70.9	79.9	30.8	14.35	11.45	11.05
SEG 40-79							100	7.6	1.6	8.3	0.7	6.7	0	0	0
SEG 80-159								100	91.25	22.55	17.15	92.45	75.8	77.7	77.1
SEG ≥160									100	16.7	22.6	85.4	76.95	78.25	78.05
PC 80-159										100	75.1	19.3	0.5	2.45	2.25
PC ≥160											100	19.3	4.95	2.15	1.55
PST 80-159												100	76.25	73.55	73.35
PST ≥160													100	95.9	95.5
PSP ≥160														100	99.4
PYP ≥160															100

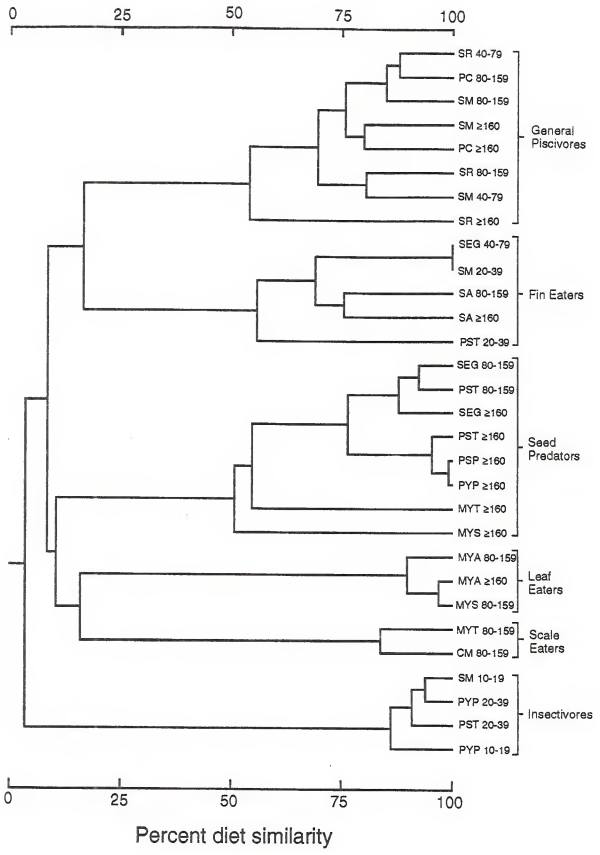
Table 6-8--continued.

Species and Size Range (SL, mm)	SA 80-159	SA ≥160	MYA 80-159	MYA ≥160	MYS 80-159	MYS ≥160	MYT 80-159	MYT ≥160	CM 80-159	SM 10-19	SM 20-39	PST 10-19	PST 20-39	PYP 10-19	PYP 20-39
SR 40-79	27	20	0	0	0	0	5.3	0.2	0	0	20	20	20	0	0
SR 80-159	47.45	44.65	5.15	5.05	5.6	6.45	18.95	9.35	14.3	0.7	31	8.95	32.05	0.7	2.9
SR ≥160	14.15	8.65	1.95	1.85	4.4	8.05	8.65	5.95	4.8	0	3.8	3.75	7.1	0	2.3
SM 40-79	36.14	30.24	1.54	1.46	2.31	2.34	6.84	2.64	1.49	0	28.7	8.3	29.06	0	2.1
SM 80-159	11.26	16.55	12.65	13.15	13.11	7.05	17.15	13.55	10.31	0.01	4.1	4.06	4.46	0	2.3
SM ≥160	9.15	14.25	24.75	17.35	16.2	19.85	16.85	26.05	10.7	0	1.4	1.45	1.85	0	2.4
SEG 40-79	63.1	75	0	0	0	0	5.3	0	0	0	100	8.3	55.3	0	0
SEG 80-159	19	12.1	11.9	3.1	1.75	49.2	9.8	55.7	4.85	0.4	7.6	8.3	22.1	0.4	1.9
SEG ≥160	18.15	11.15	11.05	2.25	0	47.25	11.15	54.55	9.5	0	1.6	1.4	1.4	0	0
PC 80-159	18.15	10.95	0.1	0	0	0.95	7.95	3.05	2.6	0	8.3	8.3	8.7	0	0.5
PC ≥160	23.35	22.55	9.45	9.35	11.9	6.25	25.55	14.15	24.8	0	0.7	0.7	0.7	0	1.6
PST 80-159	14	12.35	16.55	7.85	6.7	53.65	10.95	57.15	5.6	0	6.7	6.7	7.1	0	2.3
PST ≥160	0.5	5	15.5	6.7	4.55	51.7	5	55.4	4.95	0	0	0	0	0	1.6
PSP ≥160	2	2.2	11.4	2.6	0.45	48.7	2.2	52.8	2.15	0	0	0	0.4	0	1.0
PYP ≥160	1.8	1.6	11	2.2	0	48.3	1.6	52.2	1.6	0	0	0	0.4	0	0.6

Table 6-8--continued.

Species and Size Range (SL, mm)	SA 80-159	SA ≥160	MYA 80-159	MYA ≥160	MYS 80-159	MYS ≥160	MYT 80-159	MYT ≥160	CM 80-159	SM 10-19	SM 20-39	PST 10-19	PST 20-39	PYP 10-19	PYP 20-39
SA 80-159	100	75.6	0.1	0	0.75	0.5	32.3	4.5	29.45	2.5	63.1	10.8	58	2.5	2.6
SA ≥160		100	12.6	12.5	12.55	6.3	30.3	16.4	22.85	0	75	8.3	55.3	0	1.6
MYA 80-159			100	91.2	89.05	17	21.1	55.6	10.45	0	0	0	0	0	1.6
MYA ≥160				100	96.95	8.2	21	46.8	10.35	0	0	0	0	0	1.6
MYS 80-159					100	6.05	21.05	45.35	10.9	0.55	0	0.55	0.55	0.6	2.2
MYS ≥160						100	6.3	53.4	6.25	0	0	0	0.4	0	2.3
MYT 80-159							100	24.9	84.05	0	5.3	5.3	5.3	0	1.6
MYT ≥160								100	14.25	0	0	0	0.2	0	1.8
CM 80-159									100	8	0	7.95	7.95	8.0	9.5
SM 10-19										100	0	90	44.3	84.8	94.0
SM 20-39											100	8.3	55.3	0	0
PST 10-19												100	52.6	86.5	91.6
PST 20-39													100	44.3	44.6
PYP 10-19														100	88.4
PYP 20-39															100

Fig. 6-5. Dendrogram from cluster analysis depicting similarities among diets of piranhas and related species (by size class) from the upper Orinoco River basin, Venezuela. Similarity values are from Table 6-7, dendrogram UPGMA-generated using overlap index of Schoener (1970) and eleven resource categories. See Table 3-1 for species abbreviations.


0
25
50
75
100
SR 40-79
PC 80-159
SM 80-159
SM ≥160
PC ≥160
SR 80-159
SM 40-79
SR ≥160
General Piscivores
SEG 40-79
SM 20-39
SA 80-159
SA ≥160
PST 20-39
Fin Eaters
SEG 80-159
PST 80-159
SEG ≥160
PST ≥160
PSP ≥160
PYP ≥160
MYT ≥160
MYS ≥160
Seed Predators
MYA 80-159
MYA ≥160
MYS 80-159
Leaf Eaters
MYT 80-159
CM 80-159
Scale Eaters
SM 10-19
PYP 20-39
PST 20-39
PYP 10-19
Insectivores
0
25
50
75
100
Percent diet similarity

of the three *Myleus* species. Cluster VI was comprised of insectivores and consisted of small juvenile piranhas that fed on the larva of small aquatic insects.

Of the six different feeding guilds recognized for serrasalmine fishes from the upper Orinoco, piranhas were represented in four. None of the piranhas was considered to be leaf-eaters or scale-eaters. My results indicate that most piranhas eat scales on occasion, but none did so consistently, or to any great degree. Only in the non-piranha serrasalmines, *Catoprion mento* and *Myleus torquatus* (80-159 mm SL), did scales make up a high proportion of total diet volume. Adults of a few Orinoco piranhas were considered to be truly herbivorous, and these fed mostly on seeds. Nevertheless, most species exhibit some flexibility in feeding behavior, species considered to be primarily herbivorous occasionally took animal prey, and the more carnivorous species sometimes fed on plant material in bulk. In contrast to seed-eating piranhas, other primarily herbivorous serrasalmine fishes exploited a more varied plant diet, frequently feeding on leaves and flowers, in adddition to seeds and fruits.

Diet width measures diversity and evenness of resource use. Diet breadth usually changed with age (Fig. 6-6), but there was no consistent pattern among species. The lowest diet breadth values were found in both small and large size classes of piranhas. *Serrasalmus rhombeus* ≥160 mm SL, Group V, had the highest diet breadth (i.e., 2.99).

In summary, of the eight piranha species found in the upper Orinoco River basin: the adults of four species (*Serrasalmus rhombeus*, *S. manueli*, *S. altuvei*, and *Pygocentrus caribe*) fed heavily on fish or fish fins; and adults of the other four piranha species (*Serrasalmus* cf. *eigenmanni*, *Pygopristis denticulatus*, and two *Pristobrycon* species) were basically seed predators, biting seeds into small fragments before ingesting them. Of the three most abundant species in my samples (*Serrasalmus rhombeus*, *S. manueli*, and *S.* cf. *eigenmanni*), two were primarily piscivores, but *S. manueli*, though primarily a fish-eater, occasionally took seeds or fruits in mass. All drainages in the upper Orinoco are heavily

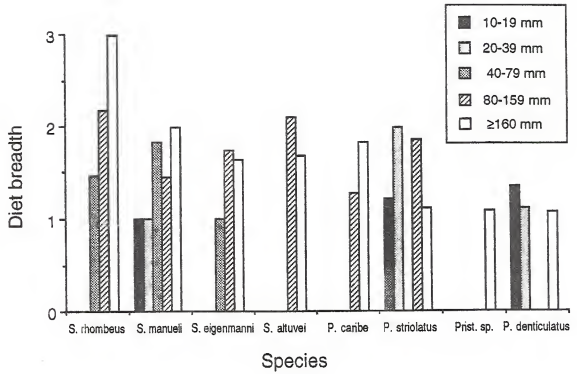


Fig. 6-6. Diet breadths estimated for eight piranha species, by size class, from the upper Orinoco River basin, Venezuela. Diet breadth calculated using formula of Levins (1968). Most species not represented in all size classes. Size ranges are standard length (mm).

forested and I found evidence of herbivory (i.e., seed-eating) by piranhas in all six drainages studied.

Data on diets of the smaller size class piranhas from the upper Orinoco is incomplete. Stomach contents of five species (<80 mm SL), supplemented by my observations on feeding behavior of wild-caught juveniles of *Serrasalmus manueli* and *Pygopristis denticulatus* kept in aquaria, suggest that most species in the upper Orinoco pass through a growth stage, between 20 and 80 mm SL, when fin-eating is common or even their predominant mode of feeding. Smaller juveniles (< 30 mm SL) taken in the upper Orinoco had fed heavily on small aquatic insects; microcrustaceans only accounted for a small part of their diets. Young piranhas rarely ate seeds or other plant matter.

Comparison with Savanna Populations

Much of my original data on the trophic patterns of savanna populations comes from the low Llanos of the Apure River basin. As seen in the previous chapter, information on the Caño Caicara area, an Apure River tributary, contrasted sharply with my findings on adult piranhas from the upper Orinoco. Fish (flesh, fins, and small whole fish) was the main component of adult diets of all seven species of piranhas from the Caño Caicara region. I rarely found evidence of seed-eating by piranhas in the Caño Caicara site. The few seeds eaten were very small and probably were taken incidentally along with intended prey items. Of hundreds of specimens examined, not one stomach contained many seeds. Other plant material, such as bits of leaves, grass blades, root wads, tiny flowers, and filamentous algae, was ingested, but was of minor importance in terms of dominance and volume. *Pristobrycon striolatus* was a seed predator in the upper Orinoco, but none of the 16 *P. striolatus* from the Apure drainage had fed on seeds; however, most specimens examined were juveniles that had fed heavily on fins. A 84-mm SL juvenile, collected in Caño Maporal and kept in an aquarium, fed on small seeds and fish fins while

in captivity (*Pygopristis denticulatus*, another herbivorous piranha, is extremely rare in the Apure River drainage and has not been taken in Caño Caicara).

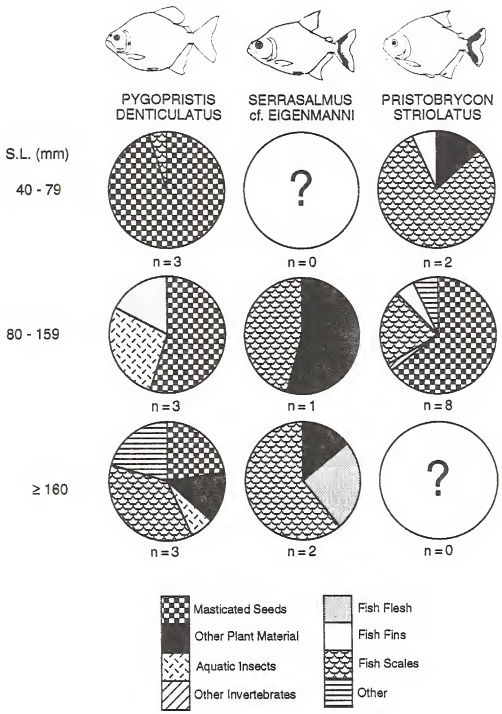
Fin eating was also common among juveniles in the Llanos. In the Caño Caicara area, the young of at least five of the seven piranha species present (i.e, *Serrasalmus rhombeus*, *S. elongatus*, *S. irritans*, *S. medinai*, and *Pristobrycon striolatus*) fed heavily on fins. The smallest juveniles (10-19 mm SL) examined from the two regions are compared in Figure 6-3. Small juvenile *Pygocentrus caribe* from the low Llanos fed on small aquatic insects and microcrustaceans in roughly equal amounts (Fig. 6-3).

The Cinaruco and Capanaparo River Drainages

Long-term research in the Caño Caicara area suggested that savanna populations of piranhas do not depend on plant material. However, my later study of fishes from savanna areas where gallery forests are more extensive suggest that differences in trophic patterns between the upper Orinoco and low Llanos are not always distinct. Although uncommon, three of the four seed-eating piranhas found in the upper Orinoco (i.e., *Pristobrycon striolatus* and *Pygopristis denticulatus*, *Serrasalmus* cf. *eigenmanni*) also occur in the Cinaruco or Capanaparo river drainages of the low Llanos. Based on a limited number of specimens taken during the dry season, stomach content analysis indicated adult piranhas of the herbivorous species feed on plant material when available in savanna situations (Fig.6-7). A description of their diets follows.

Pristobrycon striolatus was collected in both the Cinaruco and Capanaparo rivers. Two juveniles (42 and 44 mm SL) contained mostly fish fins (80% of total volume); other items included some plant material (leaf fragment and small stem) and a few scales. Larger *P. striolatus* from these two rivers were seed predators (%O-%D-%V): Group IV (n = 8, 1 empty) - masticated seeds (85.7-57.1-64.8), other invertebrates (28.6-0-2.0), fish fins (28.6-0-5.4), fish scales (57.1-42.6-21.0), other (14.3-0-6.8).

Fig. 6-7. Diets by size class (≥40 mm SL) of three piranha species from the Cinaruco and Capanaparo river drainages of the low Llanos, Orinoco River basin, Venezuela. Size of segments represents percentage of volume of each prey type; n = number of stomachs examined; numbers in parentheses represent diet breadth using formula of Levins (1968).


PYGOPRISTIS DENTICULATUS
SERRASALMUS cf. EIGENMANNI
PRISTOBRYCON STRIOLATUS
S.L. (mm)
40 - 79
80 - 159
≥ 160
?
n = 3
n = 0
n = 2
n = 3
n = 1
n = 8
n = 3
n = 2
?
n = 0
Masticated Seeds
Other Plant Material
Aquatic Insects
Other Invertebrates
Fish Flesh
Fish Fins
Fish Scales
Other

I examined the stomach contents of 11 *P. denticulatus* (19-195 mm SL) taken from the Capanaparo River drainage during low water (Fig. 6-7). Two small juveniles (19 and 28 mm SL) contained mostly microcrustaceans (ostracods, cladocerans, and copepods); other food items included aquatic insect fragments (e.g., odonata nymph) and a few diatoms. Masticated seeds were found in the stomachs of five of the eight specimens greater than 40 mm SL; food items were as follows (%O-%D-%V): Group III (n = 3) - masticated seeds (100.0-66.7-95.0), and fish scales (66.7-33.3-5.0); Group IV (n=3)- masticated seeds (66.7-66.7-55.0), aquatic insects (adult coleoptera) (66.7-33.3-27.5), fish flesh (33.3-0-17.2), and fish scales (33.3-0-0.3); Group V (n = 3) - masticated seeds (33.3-0-22.7), plant material (woody fiber and twigs) (66.7-33.3-22.7), aquatic insects (adult coleoptera) (66.7-0-6.8), fish scales (66.7-33.3-36.4), and other (soil) (33.3-33.3-11.4).

Serrasalmus cf. *eigenmanni* occurs in the Cinaruco River of the Llanos. It appears to be scarce, however, and I only examined three specimens (155-198 mm SL) (Fig. 6-7). Two stomachs contained small amounts of leaf fragments. Other items included a few large fish scales and some fish flesh.

Spatial Variation: Herbivory versus Carnivory

Based on floristic differences between the two regions, I predicted that populations in the upper Orinoco would be more herbivorous than their savanna counterparts. Table 6-9 compares the incidence of herbivory among all piranhas (specimens ≥80 mm SL) from the upper Orinoco to those from the low Llanos. With the exception of *Serrasalmus manueli*, the proportion of piranhas containing plant matter was not significantly different between the two regions. However, comparisons combining all species, and combining all members of the genus *Serrasalmus* , were significant in chi-square tests (Table 6-9).

Table 6-9. Incidence of herbivory in piranhas (≥ 80 mm SL) as associated with the low Llanos and upper Orinoco.

Taxon	Low Llanos		Upper Orinoco		
	# With	# Without	# With	# Without	
Pristobrycon sp.			5	0	
Pristobrycon striolatus	8	2	5	0	† ($P = 0.43$)
Pygocentrus caribe	88	170	4	4	† ($X^2 = 0.31$)
Pygopristis denticulatus	4	2	1	0	† ($P = 0.71$)
Serrasalmus altuvei	2	5	2	7	† ($P = 0.61$)
S. cf. *eigenmanni*	2	1	36	8	† ($X^2 = 0$)
S. manueli	2	22	16	21	** ($X^2 = 6.93$)
S. rhombeus	4	12	9	49	† ($X^2 = 0.26$)
S. elongatus	8	17			
S. irritans	13	57			
S. medinai	13	37			
All *Serrasalmus*	44	151	63	85	** ($X^2 = 14.77$)
All piranhas	144	325	78	89	** ($X^2 = 13.18$)

* $P < 0.05$, ** $P < 0.01$, † not significant

Note: Analysis was limited to individuals ≥ 80 mm SL; each specimen containing food in its stomach was considered a sample point and scored as to whether or not it contained any plant matter. To test that upper Orinoco populations were more herbivorous than their counterparts from the low Llanos, a 2 x 2 contingency table X^2 test (one tailed, X^2 value given) was used where appropriate; if N < 40 then a Fisher exact probability test (one tailed, P value given) was applied.

Many piranhas feed on small amounts of plant material, therefore using frequency of occurrence as a measure of herbivory tends to over-emphasize the importance of small plant items that in reality may not contribute much to the overall diet. To overcome this possible bias, Figure 6-8 summarizes the diet data in terms of the degree of herbivory using three different diet measures including percent adjusted volume ($\%V_a$), percent dominance (%D), and percent frequency of occurrence (%O) (for explanation of determination see Chapter 3). Based on the data given in Figure 6-8, one-tailed Mann-Whitney U-tests were used to determine whether forest piranhas (≥ 80 mm SL), as a group, were more herbivorous than their savanna counterparts (Table 6-10). In each case (i.e., using $\%V_a$, %D, and %O) the resulting probability (P) values fell between 0.07 and 0.05. As previously mentioned, seven of the eleven piranha species were found in both the Llanos and the upper Orinoco. In five of these seven wide-ranging piranha species, plant material (in terms of $\%V_a$, %D, and %O) was greater in upper Orinoco populations than those from the Llanos (Fig. 6-8). Four species (including three herbivorous species) showed fairly substantial differences between regions. *Serrasalmus rhombeus* was the only species in which samples from forest populations contained less plant food than those from savanna sites.

Although primarily a carnivore, *Serrasalmus manueli* was one of the few Orinoco species that was relatively common in both the low Llanos (i.e., Capanaparo River drainage) and the upper Orinoco (e.g., Sipapo and Atabapo rivers) and also fed to some extent on seeds. Figure 6-9 summarizes and compares diets of *S. manueli* Llanos populations with samples from the upper Orinoco. Considering only individuals ≥ 80 mm SL having food in their stomachs, two of 24 *S. manueli* examined from the Llanos contained plant material whereas 16 of 37 individuals taken in the upper Orinoco contained seeds or other plant remains. The two Llanos *S. manueli* containing plant material in their stomach were larger than 160 mm SL.

Fig. 6-8. Comparison of the proportion of plant material in the diets of carnivorous and herbivorous piranha species (≥ 80 mm SL) from the low Llanos to those from upper Orinoco River drainages in terms of percent adjusted volume ($\%V_a$), percent dominance (%D), and percent frequency of occurrence (%O). Carnivorous species abbreviations are: Pc = *Pygocentrus caribe*; Sa = *Serrasalmus altuvei*; Sel = *S. elongatus*; Sir = *S. irritans*; Sm = *S. manueli*; Smd = *S. medinai*; and Sr = *S. rhombeus*. Herbivorous species abbreviations are: Pst = *Pristobrycon striolatus*; Psp = *Pristobrycon* sp.; Pyp = *Pygopristis denticulatus*; and Seg = *Serrasalmus* cf. *eigenmanni*. Psp was found only in the upper Orinoco; Sel, Sir, and Smd were found only in the Llanos.

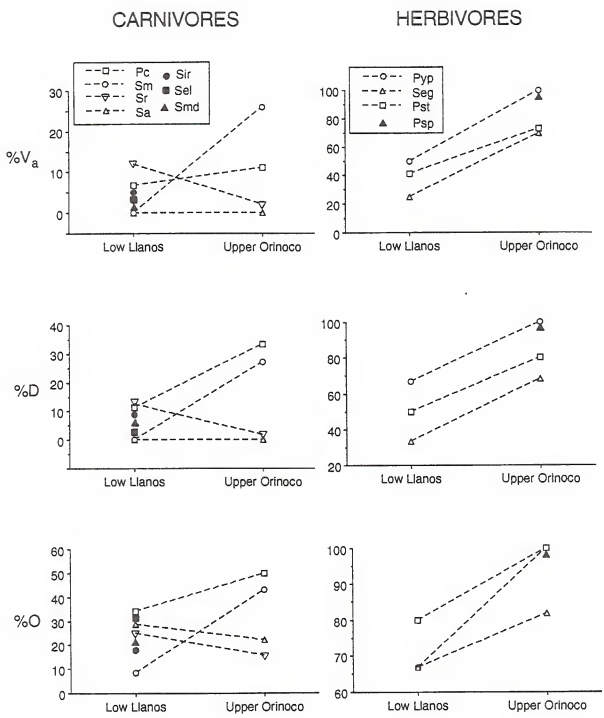
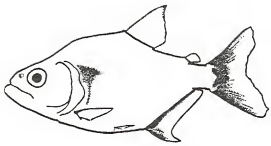

CARNIVORES
HERBIVORES
Pc
Sm
Sr
Sa
Sir
Sel
Smd
Pyp
Seg
Pst
Psp
%Va
%D
%O
Low Llanos
Upper Orinoco

Table 6-10. One-tailed Mann-Whitney *U*-test results testing the prediction that piranha species (≥ 80 mm SL) from upper Orinoco River drainages are more herbivorous than those from the low Llanos. Diet measures are percent adjusted volume ($\%V_a$), percent dominance (%D), and percent frequency of occurrence (%O) (see Chapter 3 methods for explanation). N_1 = number of piranha species from upper Orinoco; N_2 = number of piranha species from low Llanos. See Table 6-9 for number of specimens examined for each species.

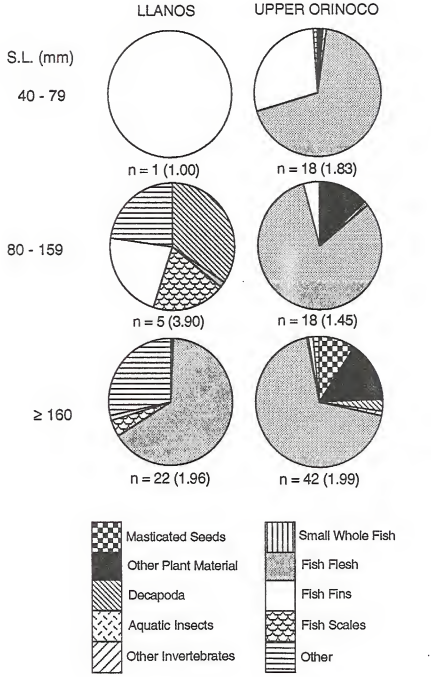
Diet Measure	N_1	N_2	*U*	Mean	SD*	*z* value*	*P*
$\%V_a$	8	10	23	40	11.22556	- 1.514402	0.0655
%D	8	10	22.5	40	11.21973	- 1.559752	0.0594
%O	8	10	23	40	11.21556	- 1.514402	0.0655

*Corrected for ties

Fig. 6-9. Diets by size class (≥40 mm SL) of *Serrasalmus manueli* comparing Llanos (Cinaruco River drainage) and upper Orinoco populations. Size of segments represents percentage of volume of each prey type; n = number of stomachs examined; numbers in parentheses represent diet breadth using formula of Levins (1968).



SERRASALMUS MANUELI



Ecomorphological Correlates: Intestine Length and Diet

In general, intestine length (IL) was positively correlated with standard length (SL), that is, the IL/SL ratio typically increased with greater body size, or age, in most species. Small juvenile piranhas tended to have fairly low IL/SL, usually less than 1.0. To reduce the effect on variability due to body size the following comparisons were limited to larger specimens, those ≥80 mm SL. Relative intestine length (IL/SL) among the serrasalmine fishes (≥ 80 mm SL) examined ranged from less than 1.0 to greater than 3.0. Differences among species were correlated with adult diet (Fig. 6-10). The association between intestine length and degree of herbivory among species (≥ 80 mm SL) was significant (Spearman rank correlation, $r_S = 0.79$, $P < .001$, $n = 35$; Fig. 6-11); carnivorous species have a short intestine (<1.5 IL/SL) and all herbivorous species have a relatively long intestine (usually >1.5). In a few cases data seemed to indicate differences in IL/SL between populations of the same species, but such variation was usually associated with small sample size or body size effects.

Large sample sizes for the three most common piranhas in the upper Orinoco (i.e., (*Serrasalmus rhombeus*, *S. manueli*, and *S.* cf.*eigenmanni*) permitted a more detailed analysis of IL, SL, and diet relationships (Fig. 6-11). *Serrasalmus* cf. *eigenmanni*, a species that fed heavily on seeds, had the longest relative IL; its IL/SL ratio was significantly greater than that of the other two species (ANCOVA; $F = 21.44$ and 26.09, $P = 0.0001$). *Serrasalmus rhombeus*, the most carnivorous of the three, had the relatively shortest intestine, whereas *S. manueli* had an intermediate intestine length. The latter species occasionally takes seeds or fruit in large quantity. Although slopes of the IL/SL regression lines did not differ between *S. rhombeus* and *S. manueli* ($F = 3.24$, $P = 0.0741$), the IL of the two species differed after adjusting for differences in SL ($F = 33.89$, $P = 0.0001$); *S. rhombeus* had a shorter intestine, as expected from its diet. My data show that adult *S. manueli* from the upper Orinoco fed more on plant material than conspecific

savanna populations (Table 6-10, Figs. 6-8 and 6-9). However, in examining possible geographic variation in the IL/SL of *S. manueli*, I found no significant difference in the slopes of the IL and SL regression lines ($F = 0.67$, $P = 0.4157$) between forest and savanna populations (Fig. 6-12).

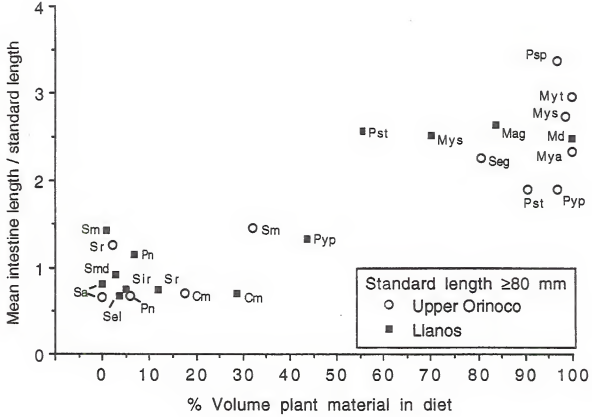
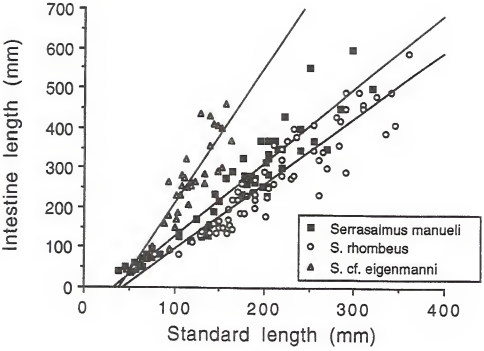
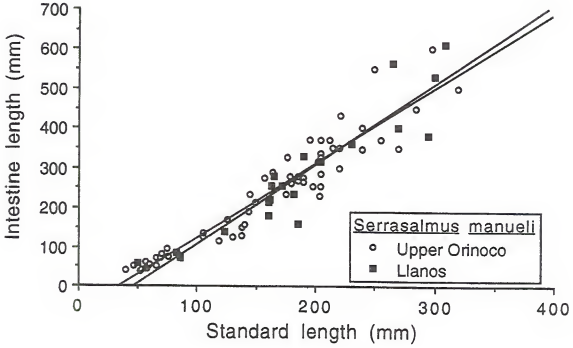


Fig. 6-10. Scatter diagram showing relationship between mean intestine length/standard length (not adjusted for SL) and percent volume of plant material in diet for selected serrasalmine fish (≥80 mm SL). Piranha species: Pyp = *Pygopristis denticulatus*; Sa = *Serrasalmus altuvei*; Seg = *S.* cf. *eigenmanni*; Sel = *S. elongatus*; Sir = *S. irritans*; Sm = *S. manueli*; Smd = *S. medinai*; Sr = *S. rhombeus*; others: Cm = *Catoprion mento*; Mag = *Metynnis argenteus*; Mya = *Myleus asterias*; Mys = *M. schomburgki*; Myt = *M. torquatus*; and Md = *Mylossoma duriventris*.

Fig. 6-11. Scatter diagram showing relationship between intestine length (IL) and standard length (SL) for the three most common piranhas in samples from the upper Orinoco River basin of Venezuela. Regression lines are as follows: *S. manueli* IL = -64.09 + 1.86SL (r^2 = 0.908, n = 60), *S. rhombeus* IL = -76.07 + 1.66SL (r^2 = 0.857, n = 70), *S.* cf. *eigenmanni* IL = -137.88 + 3.44SL (r^2 = 0.733, n = 32). Lines fitted by the above linear regression equations. r = Pearson correlation coefficient. See Appendix B for ANCOVA analyses.

Fig. 6-12. Scatter diagram showing relationship between intestine length (IL) and standard length (SL) for *Serrasalmus manueli* comparing upper Orinoco and Llanos populations. Regression lines are as follows: Upper Orinoco IL = -64.09 + 1.86SL (r^2 = 0.908, n = 60), Llanos IL = -94.32 + 2.00SL (r^2=0.864, n = 20). Line fitted by the above linear regression equation. r = Pearson correlation coefficient. See Appendix B for ANCOVA analyses.


Intestine length (mm)
700
600
500
400
300
200
100
0
0
100
200
300
400
Standard length (mm)
Serrasalmus manueli
S. rhombeus
S. cf. eigenmanni


Intestine length (mm)
700
600
500
400
300
200
100
0
0
100
200
300
400
Standard length (mm)
Serrasalmus manueli
Upper Orinoco
Llanos

CHAPTER 7
ANALYSIS OF NUTRIENT VALUES OF PIRANHA PREY

Piranhas and their close relatives exploit a broad range of food resources, including arthropods, fishes and other vertebrates, fish fins and scales, carrion, seeds, fruits, leaves, and flowers (Goulding 1980, Sazima 1983, Sazima and Guimarães 1987, Nico and Taphorn 1988, Winemiller 1989a, Sazima and Machado 1990). These diverse food items differ in terms of protein, lipid, carbohydrate and caloric content, offering piranhas a range of foods that differ in nutrient quality and digestibility. The nutrient value of a particular type of food item, along with its relative availability and digestibility, is an important factor in food preference or selection.

My results from the chemical analysis of scales, fins, and small whole fish are given in Table 7-1 and Figure 7-1. I also present some information from the literature on the energy contents and chemical components of other types of general food items, for example insects and various types of plant material.

Animal Matter

Scales

Scale-eating, or lepidophagy, is known for several unrelated freshwater fishes of South America (Roberts 1970, Sazima 1983). Many of the serrasalmine species that I examined took scales in small quantities, but *Catoprion mento* was the only species in which individuals of all sizes fed heavily on scales. The stomachs of several specimens of *Myleus torquatus* of size class IV were packed with scales, but the few specimens available

Table 7-1. Estimates of the lipid, protein, ash, carbohydrate, and caloric contents of fins, scales, and whole fish for two taxa of typical piranha prey fish. Energy expressed as kJ/g of dry mass, all others given as percent of dry mass. Where number of replicates exceeds one, values represent mean ± standard error with number of replicates in parentheses.

	kJ/g (dry mass)	% Protein (dry mass)	% Ash (dry mass)	% Lipids (dry mass)	% Carbohydrate (dry mass)
Cichlidae					
Whole fish	14.8 ±0.01 (2)	50.7 ± 0.05 (2)	33.3	7.0 ± 0.02 (2)	0.1 ± 0.03 (2)
Scales	9.0 ±0.01 (2)	43.5 ± 0.05 (2)	48.7	1.1 ± 0.18 (2)	5.7 ± 0.00 (2)
Fins	9.2 ±0.00.(2)	35.9 ± 0.05 (2)	56.2	3.3 ± 0.03 (2)	0.5 ± 0.03 (2)
Curimatidae					
Whole fish	14.9 ±0.00.(2)	52.2 ± 0.10 (2)	33.7	6.0 ± 0.01 (2)	0.8 ± 0.03 (2)
Scales	10.2 ±0.00.(2)	44.2 ± 0.38 (2)	48.3	0.7 ± 0.01 (2)	6.3 ± 0.03 (2)
Fins	10.9 ±0.00.(2)	34.0 ± 0.60 (2)	57.8	2.1 ± 0.03 (2)	2.5 ± 0.01 (2)
Combined					
Whole fish	14.9 ± 0.03 (4)	51.5 ± 0.44 (4)	33.5 ± 0.20 (2)	6.5 ± 0.30 (4)	0.5 ± 0.19 (4)
Scales	9.6 ± 0.36 (4)	43.9 ± 0.24 (4)	48.5 ± 0.20 (2)	0.9 ± 0.14 (4)	6.0 ± 0.17 (4)
Fins	10.1 ± 0.48 (4)	34.9 ± 0.60 (4)	57.0 ± 0.80 (2)	2.7 ± 0.37 (4)	1.5 ± 0.58 (4)

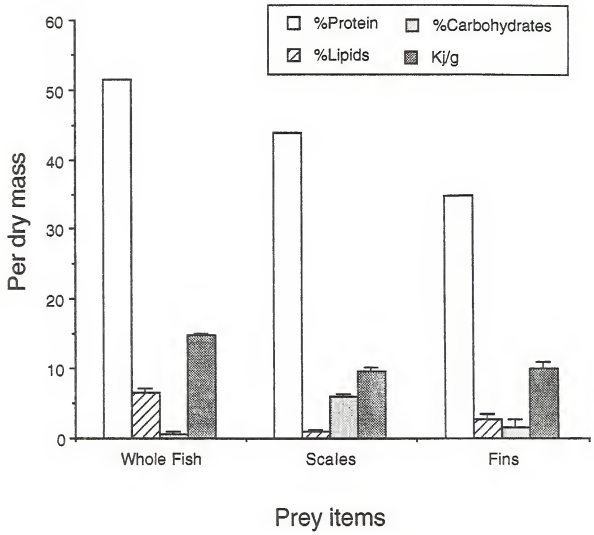


Fig. 7-1. Bar graph comparing the dry mass composition of small whole fish, scales, and fins. Energy expressed as kJ/g of dry mass, all others given as percent of dry mass. Vertical bars represent 2 SE.

made it difficult to determine if such behavior is widespread. Scales eaten were all large, thereby eliminating the possibility of intraspecific aggression since all *Myleus* species have fairly small scales.

Scale-eating fishes probably have less difficulty in digesting scales than other fish parts, for instance bone. Because I rarely found whole scales in the posterior parts of the their intestine, it suggests that ingested scales are broken down into their component parts in the foregut. Although scales are a common food item, there have been no published reports on the nutrient value of scales of South American freshwater fishes. My results from analysis of scales from cichlid and curimatid fishes generally agree with previous findings (Table 7-1, Fig. 7-1). Whitfield and Blaber (1978) reported that scales from the mugilid *Mugil cephalus*, a wide-ranging species of both marine and fresh waters, had a caloric value of 8.5 kj/g. Scales that have been studied were found to contain 40-85% protein (van Oosten 1957). The mucus that coats fish scales is rich in proteins (Wessler and Werner 1957) and lipids (Lewis 1970). In salmon, the protein content of the mucus is 62% of the dry weight (Harris and Hunt 1973). The mineral proportion, calcium phosphate, of a teleost scale ranges from 16% to 59%, depending on species (Whitear 1986). Sazima (1983) thought that scale eaters must augment their diet with other kinds of food. Goulding et al. (1988) found that 100 of 250 fish species from the Rio Negro fed on scales, usually in small quantities, and they argued that occasional scale eating may act to supplement diets for those fishes inhabiting rivers that are poor in calcium and phosphorous (e.g., blackwater habitats).

Fins

Fin eating is common among piranhas and several other South American fishes. Most fishes taken in the low Llanos are missing pieces of their caudal or dorsal fins during both high and low water periods. On the other hand, my observations seem to indicate that the incidence of fin eating is much less in the upper Orinoco (L. Nico, unpublished data).

There have been no previous studies of the nutrient content of fins as relates to fin-eating fishes. My results show that the energy and protein content of fins and scales are very similar, about 10 kj/g and approximately 34% protein (Table 7-1, Fig. 7-1). Like scales, the fins of fishes are covered with protein-rich mucus; similar to scales they probably also contain a significant amount of calcium phosphate.

Fish and Fish Flesh

Many adult piranhas prey heavily on fishes, either biting out chunks from larger fishes, sometimes as carrion, or taking small fish whole or almost whole. Compared with feeding only on fins or scales, the nutrient advantages of such behavior are obvious because the predator gets a combination of fins, scales, and flesh. The energy, protein, and lipid contents of entire small fish are higher than those of either fins or scales (Table 7-1, Fig. 7-1). Smith (1981:90), citing Junk (1977), presented a list of the fat, protein, and ash content of 21 medium and large-sized Amazonian food fishes from a floodplain lake at low water. Protein (12.4 to 20.2%) and ash (1.0 to 5.2%) contents did not vary much; however, fat content showed wide variation among species, ranging from 0.2 to 28.8%. Fat contents also show seasonal differences since many species accumulate fat after feeding during the high-water season (Smith 1981). My values for small prey fishes showed a much higher protein content (51.5%) and ash content (33.5%) than Smith reported for large fishes, with a fat content (6.5%) within the lower part of his reported range.

Arthropods

Insects and other invertebrates are some of the richer foods in terms of nutrient value per mass. Bell (1990) reported that the dry mass composition of an average insect is 59.5% protein, 15.5% fat, 5.0% ash and 7.2% carbohydrate, and yields approximately 22 kJ/g dry mass through combustion. Ranges of 5.3 to 85.4% fat, and 12 to 29.7% kJ/g were reported, with highest values often associated with larval forms (Cummins and

Wuycheck 1971, Davis and Warren 1971, Bell 1990). The lipid and energy content of insects is much higher than that of other animal food items eaten by piranhas. Microcrustaceans, similar to insects, also yield over 20 kJ/g of dry matter (Cummins and Wuycheck 1971).

The small juveniles (usually <40 mm SL) of several piranhas were found to feed on aquatic insects, mostly ephemeropterans and chironomid larvae. *Pygocentrus caribe*, which feeds heavily on aquatic insects and some fish flesh when young, has a faster growth rate than other piranhas, such as *Serrasalmus irritans*, which feed heavily on fins as juveniles (Nico, unpublished data).

Plant Matter

There are, to my knowledge, no data available on the chemical composition of the seeds, fruits, and leaves eaten by serrasalmine fishes. As a rule, plant matter tends to be high in carbohydrates whereas animal matter is high in proteins. Nevertheless, nutrient and energy content varies considerably among different plant species and different plant parts. Plants typically accumulate nutrients and energy reserves in seeds and fruits. Seeds are particularly rich in lipids in the form of oils. My study suggests that piranhas prefer seeds and hard fruits over other plant parts (e.g., fleshy fruit, leaves, flowers). Goulding et al. (1988) felt that herbivorous fishes prefer fruits and seeds to leaves because leaves are less nutritious and frequently contain toxic compounds.

Okeyo (1989) compiled information on the composition of foods found in alimentary tracts of a wide range of herbivorous fishes showing that aquatic plants vary greatly in terms of ash, protein, lipid, carbohydrate, and energy content. Previous studies investigating nutrient quality of plant matter as it relates to animal diets in the neotropics have focused primarily on mammals and birds. Snow (1981) presented food values of fruits from 20 tropical and subtropical plant species, reporting protein, fat, and

carbohydrate contents. Giving nutrient content values as a percentage of the dry mass composition of the fruit pericarp, Snow reported ranges of 1.9 to 21.6% protein, 0.6 to 67.0 % fat, and 10.8 to 90.9% carbohydrate. Worthington (1989) found that the fleshy parts of fruits eaten by manakins, a group of neotropical frugivorous birds, typically had low nutrient concentrations. However, the energy content of fruit pulp ranged from 15 to 17 kJ/g of dry pulp. Similarly, Kerley and Erasmus (1991) reported a range of 17 to 20 kJ/g dry mass for seeds commonly eaten by African rodents.

In conclusion, because of their high sugar and oil content, the energy yield of seeds and fruits is frequently higher than that of fish flesh. Nevertheless, herbivorous species probably need to supplement their diets with animal matter. Sugars supply only calories rather than essential nutrients (see Karasov and Diamond 1988). From his research on the Gray's monitor lizard, Auffenberg (1988) concluded that fruits alone, being low in both proteins and calcium, forces vegetarian reptiles to include other items such as land snails in their diet.

CHAPTER 8
DISCUSSION AND CONCLUSIONS

In this work, I have attempted to describe the diets and trophic ecology of piranhas from contrasting environments of the Orinoco River basin. The main questions addressed in this study are: (1) Do the same species of piranhas occur in both savanna and forested regions? (2) Do diets differ, and, if so, are fish from populations in forested habitats significantly more herbivorous than their savanna counterparts? (3) How do ontogenetic changes in diet compare among species and do they correlate with regional environments? (4) Is intestinal length of piranhas and other serrasalmine fishes correlated with diet? (5) What are the nutritional benefits associated with different diets or food preferences? (6) How do diets of piranhas compare with those of other serrasalmine species? (7) What is the relationship between piranha ecology and serrasalmine phylogeny? In this final chapter, I briefly reexamine these questions in view of my results and I speculate on the findings in relation to mechanistic, ecological, and evolutionary issues.

Composition of Piranha Assemblages

It it difficult to determine with certainty the precise effect ecological conditions have had on current piranha abundance and distribution patterns. Gilbert (1980) considered both historical and ecological elements as being equally important in interpreting the geographical distributions of most freshwater fishes. Along these same lines, Burr and Page (1986) suggested that similarities in fish faunal compositions among North American streams were dependent upon several factors, for instance drainage size and proximity,

geological history, and the physical and biological characteristics of the individual drainages. A combination of all these factors has probably helped to shape the distribution patterns observed for Orinoco piranhas.

Several recent studies in different parts of the Orinoco River basin have examined patterns of fish distribution and species composition. Based on long-term collecting, much of it in the Apure River drainage, Taphorn (1990) felt that altitude (lowland versus montane) and water type (i.e., clear and black versus white) were the two basic environmental parameters governing fish species distribution. He found that many species (47 of 103 characiform fishes) living in black waters seemed to be restricted to that type of habitat, whereas relatively few species were limited to just white waters (15 of 77 characiform species). In a study of fish communities from 20 floodplain lakes in the lower Orinoco, Rodríguez and Lewis (1990) found that differences in species composition between lakes might be best explained in terms of variation in small-scale factors (e.g., water type, lake morphology, and vegetation), and that apparent differences among regions might be averaged out and disappear if many sites (i.e., habitats) from each region were included in a comparison. Chernoff et al. (1991) rejected both ecological segregation and the possibility of sampling artifact and concluded that historical events, or vicariance, better explained the seemingly disjunct distribution patterns seen with some Orinoco fish species.

I examined and compared piranha distribution patterns among regions and drainages to reveal any associations existing between species composition and habitat. My interest in habitat-dependent piranha distribution revolved around their relationship to piranha trophic ecology. Although piranhas exhibit a fair amount of flexibility in what they eat, my study documents the fact that Orinoco piranhas, in terms of adult diets, nevertheless fall into two general categories: species that are largely carnivorous, and others that are primarily herbivorous (Table. 8-1). Given this apparent dichotomy in feeding preferences, a close association between piranha distribution patterns and habitat type might be predicted. Herbivorous species should be much more common in the

forested upper Orinoco drainages where plant foods, especially fruits and seeds, are an abundant and fairly reliable resource; and carnivorous species should predominate in the grassland savannas of the low Llanos where fish biomass is high but plant food availability extremely seasonal and therefore a less dependable resource.

Low Llanos versus Upper Orinoco

During this study, eleven piranha species were recorded from the two regions of the Orinoco River basin: ten from the low Llanos, and eight from the upper Orinoco. Seven species were found to inhabit both regions. Thus, even though the Llanos and upper Orinoco have very different vegetation, they are very similar in their overall piranha species composition. The high similarity in species make-up suggests that, in terms of piranhas, there are really no distinct savanna versus forest species assemblages. These results at first seem contrary to the already mentioned possibility that piranhas are distributed based on their feeding preferences (i.e., carnivorous species in the Llanos and herbivores in the upper Orinoco). However, a few exceptions to the prevailing species overlap should be noted. Four of eleven species were limited to one or the other region: *Pristobrycon* species is a seed-eating piranha known only from forested blackwater habitats of southern Venezuela; and Orinoco *Serrasalmus elongatus*, *S. irritans*, and *S. medinai*, all highly carnivorous, were taken only in the Llanos.

My findings on the relative abundance of species in the two regions suggested patterns not evident from analysis of presence-absence data alone. Several species are much more common in one region than the other. These differences were associated, in part, with differences in food resources. For example, the seed-eating *S.* cf. *eigenmanni* was rare in samples from the Llanos but common in several drainages in the upper Orinoco; the carnivorous *Pygocentrus caribe* is abundant throughout much of the Llanos but uncommon in the upper Orinoco. Overall, herbivorous species were only really cómmon

Table 8-1. Orinoco River basin piranhas categorized by adult diet (L = Llanos; U = upper Orinoco).

Largely Carnivorous	Largely Herbivorous
Pygocentrus caribe (L, U)	*Pygopristis denticulatus* (L, U)
Serrasalmus altuvei (L, U)	*Serrasalmus* cf. *eigenmanni* (L, U)
Serrasalmus elongatus (L)	*Pristobrycon striolatus* (L, U)
Serrasalmus irritans (L)	*Pristobrycon* sp. (U)
Serrasalmus manueli (L, U)	
Serrasalmus medinai (L)	
Serrasalmus rhombeus (L, U)	

the upper Orinoco. Carnivorous piranha species were abundant in both the upper Orinoco and the low Llanos, but they were more common in the Llanos.

Ecological Considerations

There seems to be no single habitat parameter that will reliably predict the makeup of piranha assemblages in given areas. Nevertheless, local ecological conditions are probably more important than regional differences in determining species abundance and local species composition. Various ecological factors, both physical (e.g., water temperature, clarity, pH, stream gradient) and biological (e.g., vegetation, availability of food, spawning requirements, symbiotic interactions with other organisms) can be considered as potentially limiting numbers and kinds of piranhas. Some of these factors have already been touched upon briefly in the preceding sections.

Most Orinoco piranha species, in addition to being widespread, are found in a variety of lowland habitats (e.g., rivers, streams, floodplain lagoons and oxbow lakes) over a wide range of environmental conditions (Table 4-4). If numbers of individuals can be used as an indicator of habitat quality, then the preferred habitats of most species are lentic white waters. *Serrasalmus* cf. *eigenmanni* is the most common herbivorous species in the upper Orinoco, and it was found in both whitewater streams and cutoff meanders. Carnivorous piranha species seem more able than herbivorous species to adapt to perturbation. For example, several of the more carnivorous species occur in great numbers in reservoirs: *Serrasalmus rhombeus* and *Pygocentrus caribe* in the Orinoco (personal observations), *S. rhombeus*, *S. spilopleura*, and *P. nattereri* in Brazil (Table 1-1). To my knowledge, those species that I have categorized as largely herbivorous (Table 8-1) are never found in reservoirs. Still, many species are apparently able to maintain smaller populations in what might be described as less desirable habitats.

Several species are widely distributed but seem to be uncommon throughout their ranges (e.g., *Serrasalmus altuvei*, *Pristobrycon striolatus*, *Pygopristis denticulatus*).

Serrasalmus altuvei has been found recently in the Rio Negro of the Amazon basin where, as in the Orinoco, it is also considered quite rare (Jégu and Santos 1987, Jégu et al. 1991). Explanations for the noted natural rarity of these species may be found, perhaps, in their having more specific habitat requirements (see Gilbert 1980). Some of the more uncommon species of piranhas seem to have somewhat specialized diets as adults, and a narrow food preference might account for their low numbers. For example, adult *S. altuvei* are basically fin eaters, and some of the other rare piranha species are mainly herbivorous. (See later discussion of dietary specialization).

Species closely related to piranhas (e.g., *Colossoma*, *Piaractus*, *Mylossoma*) are known to make long seasonal migrations of many hundreds of kilometers for purposes of tracking food resources or for reproduction (Lowe-McConnell 1964, Goulding 1980). In contrast, migratory movements by piranhas seem limited to lateral movements across the floodplain and to short seasonal journeys between more permanent waters (large streams and lagoons) and their floodplains. Field researchers have yet to observe piranhas spawning in the wild or even identify precisely where eggs are deposited (but see Lowe-McConnell 1964). In all likelihood, spawning sites are located in aquatic vegetation. My unpublished data on the reproductive condition of adults and monthly differences in body size indicate that spawning takes place mainly during the early part of the rainy season. Small juvenile piranhas are always found in flooded vegetation and it has been shown that they use macrophytes for both shelter from predators and as a foraging area (Menezes et al. 1981, Sazima and Zamprogno 1985, Nico and Taphorn 1988, Nico 1990, this study). The upper Orinoco has few habitats with large areas of aquatic macrophytes and this scarcity may limit piranha numbers in that region.

In addition to regional differences, differences in species composition and abundance among habitats within regions also seem to be associated, at least in part, with differences in types and availability of food resources. Perhaps the clearest example is that from the Llanos. Earlier work in the Caño Caicara area suggests that all Orinoco savanna

piranhas are basically carnivorous (Nico and Taphorn 1988, Winemiller 1989a, see Chapter 5). However, my later research of piranhas in other low Llanos drainages gave evidence of seed eating by adults of two, and perhaps three, savanna species. The savanna drainages studied (Apure, Cinaruco, and Capanaparo) are all located in the low Llanos of Apure State; but study sites in the Cinaruco and Capanaparo drainages differed somewhat from the Caño Caicara site of the Apure River drainage in having large gallery forests. Similar to the flooded forests of the upper Orinoco, savanna regions having extensive gallery forests provide a significant amount of edible plant material during high-water periods when fishes are able to move across their floodplains; but plant foods are rarely available to savanna fishes during the dry season when water levels have dropped. This fact alone may explain why the more herbivorous piranha species are not very common in savanna drainages. Admittedly, quantitative studies of availability of food resources across a range of habitats are still required.

The possibility that South American fishes might segregate according to water type is an attractive idea, only partly supported by recent field work (e.g., Taphorn 1990, Rodríguez and Lewis 1990). Nine of the 11 Orinoco piranha species studied were either found in two or in all three major water types (Table 4-4). Nevertheless, as found by Taphorn (1990) in his study of Apure River fishes, blackwater habitats have a more unique fish fauna than whitewater habitats due to a fairly high proportion of endemics or core species. Even though few species are restricted to a particular water type, there do appear to be consistent differences in relative abundance between water types for those species that inhabit both black and white waters. Whereas most piranha species reach their greatest numbers in whitewater habitats, several Orinoco species (i.e., *Serrasalmus manueli*, *Pygopristis denticulatus*, *Pristobrycon* sp.) are apparently restricted to, or much more common in, black waters. In my study, cluster analysis of drainages based on species composition also tended to group drainages that were similar in habitat (e.g., water type), as well as by their geographic proximity.

Given the complex situation of various water types superimposed onto both savanna and forested regions, exceptions to any generalizations can be found. Nevertheless, although additional studies are needed, some general trends are apparent that are obviously important in understanding the trophic ecology of serrasalmine fishes. On average, it seems safe to assume that aquatic primary production is greater in the Llanos than in the upper Orinoco (see Saunders and Lewis 1988), and is greater in white water than in either blackwater or clearwater situations (Fittkau et al. 1975, Saunders and Lewis 1988, Goulding et al. 1988). Of course, white waters are much more common in the Llanos than in the upper Orinoco. Furthermore, my observations indicate that white waters in the upper Orinoco are less turbid and correspondingly less productive than those of the Llanos. In any case, South American fishes inhabiting highly productive waters feed more on autochthonous foods (e.g., aquatic insects, fishes, and so on), whereas fishes inhabiting nutrient-poor waters depend more on allochthonous material for food (e.g., fruits, seeds, leaves, and terrestrial and arboreal insects).

Historical Perspective

It is interesting to speculate as to what effects past climatic changes might have had on the distribution and abundance of piranhas and other serrasalmine fishes. Herbivorous serrasalmine fishes existed more than 15 million years ago during the Miocene, long before the start of the Quaternary (Lundberg et al. 1986). As described in Chapter 2, the equatorial lowland regions of South America experienced dryer and hotter climates during major glaciations resulting in an expansion of savanna and open-land environments. Because humid forests would have contracted in size, herbivorous serrasalmines would either have had to adjust to changes in food, or been forced either to retreat to the remaining forested regions or to maintain close ties to rivers with large gallery forests. On the other hand, interglacial or pluvial periods were wetter and relatively cooler, contributing to the expansion of humid forests, a situation clearly favoring herbivorous fishes.

Based on the fossil record and the proposed phylogenetic relationships among serrasalmine fishes (Lundberg et al. 1986; Fig. 1-1), no less than a proto-piranha existed before the start of the Pleistocene. If this "first piranha" entered the Quaternary unchanged, subsequent radiation might have been in the form of adaptive responses to the dramatic changes wrought by glacial events. In this scenario, herbivorous piranhas would have evolved in forested areas and perhaps certain carnivorous forms in savanna regions. However, given evolutionary stasis (see Lundberg et al. 1986) and the possibility that piranhas, as we now know them, had already evolved well before the climatic events of the Pleistocene, piranha lifestyles would still have been dramatically altered by the climatic cycles, and these fishes would have had to respond behaviorally, if not morphologically, to large cyclical changes in food resources.

Trophic Patterns

Trophic Groupings

Based mostly on stomach content analysis, I identified six general trophic groups among the serrasalmine fishes and size classes studied; four of these six feeding guilds included piranhas. In order to compare the Low Llanos and the upper Orinoco groupings, I attempt a general assessment in the following pages. Information on minor food items not included in these discussions can be found in species account sections presented earlier.

1) Piscivores. The adults of at least seven Orinoco piranhas (*Serrasalmus* and *Pygocentrus*; Table 8-1) are largely carnivorous, feeding mainly on fishes by either biting out pieces of flesh or taking small fish whole. In addition to actively preying on other fishes, piscivorous piranhas are opportunistic and scavenge on dead or dying fish (as well as other vertebrates) (see Sazima and Guimarães 1987, Nico and Taphorn 1988). Goulding (1980) reported that the dominant Amazonian piranha, *S. rhombeus*, preyed most heavily on common fishes of about its own size by removing chunks of flesh. I

found that Orinoco piranhas, particularly in low Llanos where there is greater fish biomass, frequently attack small fish.

As a group, piscivorous piranhas are often the predominant predators in lowland habitats throughout the Orinoco River basin. Even in the upper Orinoco, I found that carnivorous species (i.e., *S. rhombeus* and *S. manueli*) outnumber individuals of the more herbivorous species in most areas. The best information on numbers and biomass of Orinoco piranhas comes from two studies in the Llanos. Based on rotenone sampling in a savanna lagoon during the dry season, Mago-Leccia (1970) reported that piranhas (mostly *Pygocentrus caribe*) accounted for 14 % of the total number of individuals and 26% of the total fish biomass. In their study of flooded savannas in the Caño Caicara area, Taphorn and Lilyestrom (1984) found that the biomass of *P. caribe* was greater than any other fish predator in both dry season and wet season samples. Their rotenone sampling of a dry season pool showed that piranhas made up 14% of total fish biomass.

2) Fin Eaters. Stomach content analysis, supplemented by my observations on feeding behavior of wild-caught juveniles, showed that most piranha species pass through a growth stage, between 20 and 80 mm SL, when fin-eating is common or the predominant mode of feeding. Fin-eating seems to be common in young of three of the four piranha genera (all except juvenile *Pygocentrus*), and includes juveniles of both herbivorous and carnivorous species from the Llanos and the upper Orinoco. At least two wide-ranging species, *Serrasalmus altuvei* and *S. elongatus*, feed heavily on fins as adults (Roberts 1970, Goulding 1980, Nico and Taphorn 1988, this study). Even though fins apparently do not provide the nutritional benefits of fish flesh (see Chapter 7), many species may eat fins because fins are an abundant and rapidly renewable resource (Northcote et al. 1987, Nico and Taphorn 1988). In cropping fins instead of eating the whole animal, piranhas resemble herbivores that continually exploit their food resource without eliminating it. Reproduction of piranhas is closely correlated with the reproductive cycle of most other fishes, thus there is an abundance of small prey available to young fin-eating piranhas.

Various tactics for successfully nipping fins from other fish have been described including aggressive mimicry (Nico and Taphorn 1986, 1988, Sazima and Machado 1990). Where piranhas are abundant, many fishes have missing or damaged fins (Northcotte et al. 1987, Nico and Taphorn 1988) making the physical condition of fishes a useful indicator of piranha density.

Defense by prey fish against fin-eating piranhas is an interesting topic and probably includes both morphological and behavioral adaptations. The fins of several South American fishes are nearly transparent in water, for instance those of the anostomid *Abramites hypselonotus* . Although there is no experimental evidence, the near transparency of their fins probably provide them protection from predation by fin eaters. Winemiller (1990) presented evidence that the caudal eyespot of the cichlid *Astronotus ocellatus* acts as a deterrent against fin predation. However, behavioral adaptations against fin-eating piranhas do not require a long history of coevolution. For example, I sometimes give live bluegill (*Lepomis macrochirus*) and other native North American fish to young aquarium-kept piranhas. In a large aquarium, small fast-swimming fishes are able to avoid predation; however, most bluegill are rapidly attacked and soon killed. Nevertheless, I have observed that a few individuals survive weeks in a large tank with a single piranha. Because fin-eating piranhas normally attack from behind and toward the rear of their prey, these longer-surviving bluegill apparently learn to protect themselves by facing the piranha and backing into dense vegetation or crevices. Thus they prevent attacks from the rear as well as possible crippling injury to their caudal fin.

3) Scale Eaters. Scale-eating, or lepidophagy, is known for several unrelated South American freshwater fishes (Roberts 1970, Sazima 1977, 1983, Sazima and Machado 1982, Goulding et al. 1988). The possible nutritional benefits of scales have already been briefly discussed in Chapter 7, and like fins, scales can be thought of as a renewable resource. Many of the serrasalmine species in both the Llanos and the upper Orinoco take scales in small quantities, but the non-piranha *Catoprion mento* is the only species in which

individuals of all sizes fed heavily on scales. It was common in the low Llanos but rare in samples from the upper Orinoco. *Catoprion mento* is a widely distributed species and its scale-eating habits are well documented (Roberts 1970, Vieira and Géry 1979, Sazima 1983, 1988, Nico and Taphorn 1988). The stomachs of several specimens of *Myleus torquatus* from the upper Orinoco were packed with scales: this is an unusual behavior not previously reported for members of this generally herbivorous genus. Although most studies suggest that adult *Serrasalmus elongatus* are primarily fin eaters (Roberts 1970) or a general piscivore (Nico and Taphorn 1988, this study), Goulding (1980) reported that adult *Serrasalmus elongatus* in the Madeira River drainage of Brazil preferred scales to fins. Based on stomach content analysis alone, it is difficult or impossible to determine which prey species are most frequently attacked. Certain species are obviously more vulnerable to having scales removed than others. For instance, while the scales of some fish are firmly attached to the body (e.g.,cichlids), the scales of others (i.e., many characoids) are easily dislodged and these fish are probably more prone to attack by scale-eaters.

4) Predation on Invertebrates. Like the young of most freshwater fishes, small juvenile piranhas (less than about 40 mm SL) commonly feed on immature aquatic insects and microcrustaceans. Most major groups of small freshwater crustaceans were represented in their diet, including cladocerans, copepods, ostracods, and conchostracans. Most aquatic insects eaten by young piranhas were immature forms of chironomids, ephemeropterans, odonates, and plecopterans. The smallest piranhas in the Llanos fed almost equally on insects and microcrustaceans, whereas small juveniles taken in blackwater areas of the upper Orinoco preyed mainly on insects. Earlier it was emphasized that there is a common association between young piranhas and aquatic vegetation. In addition to providing some protection from predators, aquatic macrophytes are home to a large number of invertebrate prey. Based on observations of wild-caught piranhas in aquarium, Sazima and Zamprogno (1985) described how young juveniles pick chironomids and ostracods from the roots of water hyacinths. Invertebrates are also taken

on occasion by adult piranhas, mostly terrestrial and flying insects, and shrimp and crabs. Braga (1954) reported that shrimp were the main prey of adult *Serrasalmus rhombeus* inhabiting a man-made lake.

5) Seed Predators. Many serrasalmine species feed on seeds and the hard parts surrounding the seed (mainly endocarp). The term "seed predator" was used by Goulding (1983) to refer to fishes that destroy seeds by mastication or other digestive processes. This is in contrast to several other basically herbivorous serrasalmids (most often *Colossoma macropomum* and *Piaractus brachypomus*) which, in addition to masticating seeds, occasionally act as seed dispersal agents by swallowing and passing whole seeds (Gottsberger 1978, Goulding 1980, 1983, personal observation). Four piranhas representing three genera (Table 8-1) were largely herbivorous and all were primarily seed predators. *Myleus* species from the upper Orinoco also sometimes feed on seeds that they bite into small fragments. Llanos piranhas rarely eat seeds, but seed predation was common among piranhas in all six upper Orinoco drainages. Goulding et al. (1988) reported that *Myleus* switch from seed-eating to folivory during low water when fruits and seeds are in shorter supply, this may be the case with Orinoco *Myleus* as well (see next section on folivores), but I found that herbivorous piranhas continued to feed on seeds even during the dryer season. Herbivorous fishes are known to gather around trees that are dropping their fruit (Goulding et al. 1988). A few carnivorous serrasalmine species are somewhat territorial (Sazima 1988, personal observation). Like their carnivorous relatives, herbivorous piranhas can be very aggressive at times and it is conceivable that they maintain feeding territories around fruiting trees during the low water season, driving away other herbivorous fishes that might compete for a limited number of seeds.

Several authors list examples of the seeds and fruits eaten by various South American fishes, including a few serrasalmine species (Gottsberger 1978, Goulding 1980, Smith 1981, Goulding et al. 1988). I was unable to identify the crushed seeds found in the stomachs of Orinoco piranhas, but a large *Piaractus* (560 mm SL) from the upper Orinoco

had its stomach and intestine full of what were probably palm seeds; about half the seeds had been masticated and the remainder, about twenty seeds (about 30 mm long) had been swallowed whole. Machado-Allison and Garcia (1986) reported that juveniles of several piranha species from a savanna marsh fed on the tiny seeds of sedges (Cyperaceae), but they did not give number of seeds eaten nor their percentage of the overall volume of food (Table 1-1).

6) Leaf Eaters. None of the Orinoco piranhas were considered to be folivores, but small bits of leaves or even flowers were eaten by all species on occasion. Of the serrasalmine species studied, only *Myleus* feeds heavily on leaves. *Piaractus* will also take leaves in bulk (personal observation). Folivorous serrasalmine fishes seem to restrict themselves to feeding on live leaves that they clip into small fragments before swallowing. Similar behaviors have been reported for leaf-eating fishes of the Amazon (Goulding 1980, Goulding et al. 1988). Goulding et al. (1988) hypothesized that folivory by Amazonian fishes is limited by the toxic chemicals in the leaves. Their studies suggest no specialized folivores among herbivorous fishes, but rather that frugivorous fishes become leaf eaters only when fruits and seeds are scarce, for instance during periods of low water. Most of the *Myleus* that I examined were captured during the low water period; therefore, I cannot rule out such a seasonal shift in diet. Nevertheless, the stomachs of herbivorous piranhas, netted together with *Myleus* taken in the upper Orinoco during the drier part of the year, were full of seeds, suggesting some sort of food resource partitioning.

Ontogenetic Changes in Diet

My study approach has been to emphasize dietary differences among different size classes as well as among species. The differences found therefore tend to support the contention of Stoner and Livingston (1984) that ecological studies of fishes should employ the "ontogenetic trophic unit" concept rather than grouping a taxonomic species as a single functional ecological unit. Changes in diet with age have been documented for many of the

Orinoco species found in the Llanos (Machado-Allison and Garcia 1986, Nico and Taphorn 1988, Winemiller 1989a, Nico 1990) and for *Serrasalmus spilopleura* from a reservoir in southern Brazil (Sazima and Zamprogno 1985) (Table 1-1). In general, piranhas change their preferred prey as they grow from invertebrates as small juveniles, to fins as large juveniles, and finally to a diet of mainly fish or plant matter. The size at which individuals switch from one mode of feeding may be species specific, related to food resource availability, or more likely, a combination of both of these factors. All juveniles less than about 20 mm SL specialize on invertebrate prey (i.e., microcrustaceans and aquatic insect larvae), some not switching to fins until about 40 mm SL. Fin eating is most common in juveniles between 40 and 80 mm SL, but I found that juveniles as small as 20 mm SL (e.g., *Serrasalmus manueli*) already begin feeding on fins taken from other small fishes. Although data are incomplete on several species, *Pygocentrus caribe* is the only common piranha that does not feed on fins to any great extent as a juvenile (but see Machado-Allison and Garcia 1986). Although some species continue to feed heavily on fins as adults, larger individuals of most species switch to a diet consisting primarily of fish or seeds. Herbivory among piranhas seems to be mainly an adult trait, whereas the young of other serrasalmine fishes (e.g., *Metynnis*) will frequently feed on plant matter. In contrast to the findings of Machado-Allison and Garcia (1986), young piranhas that I studied rarely ate seeds or other plant matter.

Carnivory versus Herbivory

Although adult piranhas may be classified as either largely carnivorous or largely herbivorous (Table 1-1), my results suggest that they can adjust their diets to changes in food resources. There is a certain amount of omnivory in both groups. However, when specimens of both groups were taken together, diets were usually distinctly different. In the upper Orinoco, when finding two or more piranha species in the same gill net, their stomachs were either full of seeds or fish flesh. Such partitioning of food resources was

usually predictable according to species. For the most part, occasional bits of plant material in the stomachs of typically carnivorous species were considered the result of accidental ingestion when these fish were attacking prey fish. However, underwater observations in the Pantanal of Brazil reported by Sazima and Machado (1990) suggested that primarily carnivorous species *Serrasalmus spilopleura* and *Pygocentrus nattereri* actively feed on leaves of aquatic plants while scanning for aquatic insects and small crustaceans.

A hypothetical model for describing piranha responses to differing environmental conditions is presented in Figure 8-1. This model shows trends and not absolute values. All piranhas exhibit a certain amount of trophic flexibility. The model shows diets of carnivorous and herbivorous piranhas to be most different when conditions provide for a roughly equal amount of plant (i.e., mainly seeds) and animal food (i.e., mainly fish), or when neither type of food is in limited supply. The vertical broken line of Figure 8-1 shows a situation I frequently encountered when both carnivorous and herbivorous species were taken together in the upper Orinoco. Like any model, it does not take into account all possible variables or conditions, but it does explain many of the findings of the present study.

During extreme conditions both trophic groups might be expected to adjust their diets, resulting in high dietary overlap (e.g., *P. striolatus* in the Apure drainage). When the availability of edible plant materials (primarily seeds) is low, there is a corresponding shift by herbivorous fishes to a more omnivorous diet. Dietary shifts by adult piranhas are likely to be associated either with temporal changes, such as from highwater to lowwater conditions, or with spatial changes, such as from a forest habitat to one that is more typical of savannas. An obvious case where such a shift might occur is a savanna lagoon during the onset of the dry season; as the pool shrinks, prey fish densities rise (at least temporarily), but the input of plant resources into the system becomes negligible. On the other hand, largely carnivorous piranhas might shift to a more omnivorous diet when the availability of plant materials increases, such as the change from low water to flood

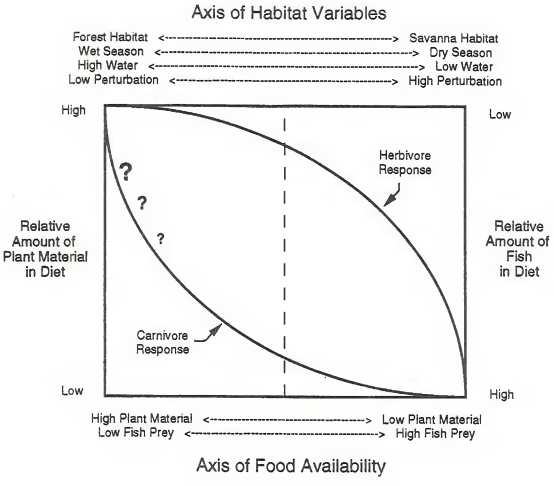


Fig. 8-1. Proposed hypothetical model showing the dietary responses of carnivorous versus herbivorous piranha species to changes in various habitat parameters and food resources. Dashed vertical line indicates the condition where both plant material and prey fish are in approximate equal supply and relatively abundant (see Table 8-1 for list of piranha species involved).

conditions, especially in forested habitats. Perhaps the best examples of carnivorous piranhas adjusting its diet to local conditions are individuals of *Serrasalmus manueli* that had fed on seeds and fruits in the flooded forests of the Sipapo River.

Generalist versus Specialist

In his analysis of avian diets, Sherry (1990) discussed the subject of specialist versus generalist from both ecological (i.e., tactical) and evolutionary (i.e., strategic) points of view, also taking into account other closely related dichotomies (e.g., stereotypy vs. plasticity, monophagy vs. polyphagy, specialized vs. opportunistic). In a study of insects, Fox and Morrow (1981) found that many herbivorous species have generalized diets over their entire geographical ranges but that they may function as specialists with restricted diets in specific areas.

Diet breadth, as estimated by Levins' index (see Chapter 3), measures the diversity and evenness of resource use. Thus, diet breadth is actually a quantitative attempt to measure the degree of dietary specialization (i.e., the resulting value being lower for a dietary specialist and higher for a dietary generalist). Unlike many dominant predators found in freshwater communities, piranhas are little limited by gape size (i.e., not gape-limited predators sensu Zaret 1980) because they use their teeth to cut out bite-size pieces even from fairly large food items. Nevertheless, because larger piranhas are able to attack or ingest a wider range of food sizes than smaller conspecifics, it would be expected that diet breadth would increase with increasing fish size.

Although I found that diet breadth among piranhas usually changed with age, there was no consistent pattern among species. The lowest diet breadth measured during my study were for species and size classes considered to be scale eaters and fin eaters, fairly specialized types of feeding behaviors. Nevertheless, species or size classes that specialize on the fins or scales of other fishes can choose to attack many different fish species and select from a wide range of prey fish sizes. In most instances, it was not possible to

identify a prey species based only on fin fragments or scales found during examination of stomach contents. However, my observations of feeding by captive fishes indicate that fin-eating and scale-eating serrasalmine fishes are capable of successfully attacking individuals of many fish species. Fin-eating piranhas use several basic tactics to approach prey fish, for instance ambushing, stalking, and active chase. Although particular species appear to be better suited morphologically for employing one tactic over another (e.g., the streamlined *S. elongatus* for active pursuit; narrow deep-bodied species such as *S. altuvei* for stalking) (Nico and Taphorn 1988, Sazima and Machado 1990), my observations indicate that the particular tactic used by individuals of a given species can vary widely and seems to depend on several factors, for example, the amount and type of cover, the density and type of prey fish, and water clarity. In nature, juvenile *Serrasalmus irritans* use aggressive mimicry to approach other fish (Nico and Taphorn 1986, 1988). However, in large outdoor tanks I have seen individuals use both ambush and pursuit. In the first case, an individual hides among rocks and ambushes passing fish; in other instances they leave their hideaway and actively pursue fish in open water over distances of more than a meter. I have kept a young wild-caught *Pygopristis denticulatus* for nearly a year in a large aquarium; it slowly stalks novel prey fish, but it will immediately chase small fish that are not novel. Based on the size of fins in their stomachs, small juveniles in nature attack fish that are about their own size; however, large fin-eating piranhas will prey on the fins of fish much larger than themselves, for example the pimelodid catfishes *Brachyplatystoma* and *Phractocephalus*.

In the Orinoco and elsewhere, studies are needed to determine to what extent herbivorous fishes specialize on particular seeds or leaves. The method of diet analysis used here, scoring plant foods as masticated seeds versus other plant material, gives low diet width values for herbivorous fishes that may be misleading. Goulding (1980, 1983) and Goulding et al. (1988) reported that herbivorous fishes in the Amazon River basin exploit a wide range of plant species, but they seem to prefer fruits and seeds of a few

common species (e.g., seeds from rubber trees and palms). Goulding (1980) was able to identify only a few seeds eaten by Amazonian piranhas. Similarly, because I could not identify the seeds and most other plant materials in the diets of Orinoco herbivorous species (i.e., adults), I cannot adequately assess their degree of specialization. Snow (1981) distinguished between specialized frugivorous birds and unspecialized or opportunist frugivores. The former typically feed on fruits rich in fats and proteins, whereas the latter mostly take fruits that provide mainly carbohydrates and less nutritious overall.

Although serrasalmine species or size classes were assigned to particular trophic guilds, all exhibited a certain amount of plasticity in their diets. Because most foods do not supply all the nutrients needed by an animal, a certain level of diet flexibility is probably a requirement. An assessment of the balance between benefits and costs of piranha particular modes of feeding and prey choice lies beyond the scope of the present study. Analysis of energy and nutrient content suggests that certain types of foods are generally more beneficial than others (e.g., fish flesh and insects over fish fins and scales, fruits and seeds over leaves), but it ignores the possible costs of foraging, and that proportion of a food item that is actually assimilated by the consumer. Each of these determinations would require further study. Comparing aquatic versus terrestrial feeding modes, Liem (1990) hypothesized that fish, by nature of their being designed for life in the water, have a much more versatile feeding apparatus (i.e., mouth and jaw structures) than terrestrial vertebrates. Based on this "built-in versatility", one of Liem's predictions was that fish should be highly opportunistic in their feeding, thereby exhibiting both high dietary overlap and extensive prey switching.

Ecomorphological Correlates

Ecomorphology examines correlations between organism morphology and selective demands of its external environment. Keast and Webb (1966) were among the first to look closely at possible relationships between fish trophic morphology and fish diets.

Piranhas have interspecific variation in body height, body width, shape of snout, and maximum size; general body shape also changes dramatically during growth in several species, for example in *Serrasalmus rhombeus* as described and figured by Géry (1972). Nico and Taphorn (1988) thought that piranhas with sharp snouts (*Serrasalmus irritans* and *S. elongatus*) were more adapted for nipping fins or taking scales but found that even a few species with somewhat blunt snouts (*S. medinai* and *Pristobrycon striolatus*) fed heavily on fins. Sazima and Machado (1990) also suggested that particular piranha body morphologies were associated with particular predatory tactics: the low profile and powerful tail of *Pygocentrus nattereri* for giving short chase, and the high fins and narrow body (in addition to a greenish body color) of the fin-eating *S. marginatus* for hiding in vegetation while stalking its prey.

Particular types of morphology or behavior can preadapt animals to their current ecological niches. For example, Futuyma (1986:424) described how a New Zealand parrot, the kea (*Nestor notabilis*), uses its beak to rip through the skin of sheep and feed on the fat beneath. The beak is similar to that of normal seed- and fruit-eating parrots, but its form presumably preadapted the kea to invade the sheep-eating niche. Piranhas have a single row of sharp, somewhat triangular teeth in both jaws used for rapid puncture and shearing. Dental morphologies exhibit only slight variation among species, and are sufficiently unspecialized that individuals are able to exploit a broad range of food. As such, the unique dentition and strong jaw musculature of piranhas preadapts them for feeding on hard seeds and fruits. This statement presumes, possibly incorrectly, that carnivory is the "primitive" ecological character state within piranhas.

Other morphological features related to feeding, for instance intestine length, show much more variation among the different piranha species. Previous investigators have noted that carnivorous fish (like many terrestrial vertebrates) have relatively shorter intestines than herbivorous fish (see Ribble and Smith 1983), suggesting a correlation between length of the gastrointestinal tract and the feeding ecology of a species (but see Smith 1989). A longer intestinal tract provides a greater surface area for digestion and absorption of difficult to digest plant material. Several researchers have even reported large intraspecific differences in intestine length among fishes. For example, Odum (1970) compared two populations of mullet (*Mugil cephalus*) and reported that the gastrointestinal tract was nearly twice as long in those fish living in a marsh habitat and feeding on hard-to-digest items such as plant detritus and blue-green algae when compared to mullet inhabiting an area where the predominant food consisted of benthic and epiphytic diatoms, a food more easily digested. Luengo (1965) noted the relationship between the carnivorous diet of *Pygocentrus caribe* (identified as *Serrasalmus nattereri)* and its relatively short intestine.

My study showed that intestinal length in Orinoco piranhas varies interspecifically and is closely correlated with diet. Dental morphology, on the other hand, is a relatively conservative character within the four piranha genera, although relative jaw width and degree of musculature vary. This contrasts with the situation present in other serrasalmine fishes, which exhibit a much more diverse dental morphology, indicating a more labile evolutionary past (Lundberg et al. 1986). The adults of most non-piranha serrasalmines are herbivorous (e.g., *Myleus*, *Mylossoma*, and *Metynnis*) and have relatively long intestines. *Catoprion mento* is an exception because it eats scales and has a short intestine. In addition, studies with other vertebrates indicate that features other than length (e.g., cellular anatomy or biochemical composition) also determine function of the digestive tract, and these characters may also show inter- and intraspecific differences (e.g., Karasov and Diamond 1988). However, I found no evidence to suggest that the intestine length of individual fish changes in response to shifts in diet.

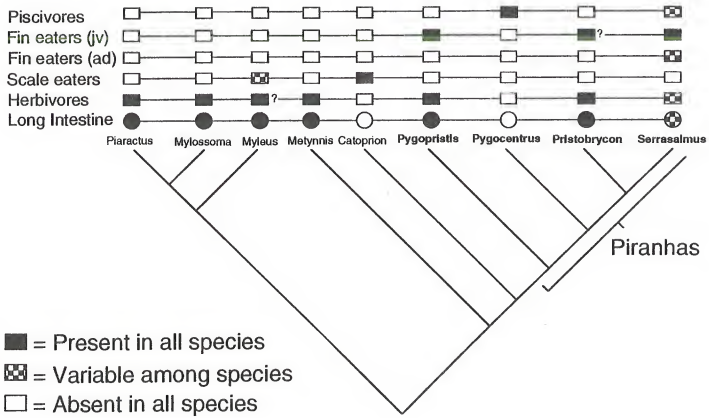
A Phylogenetic Perspective

In order to synthesize information concerning ecology and evolution, biologists commonly superimpose ecological or behavioral results onto hypothesized phylogenies derived from gross morphology or biochemical systematics (Brooks and McLennan 1991). These types of analyses are preferred because they attempt to establish correlations between the evolutionary history of organisms and present-day patterns of morphology, behavior, and ecology. Nevertheless, as Losos (1990) has suggested, meaningful analysis in a phylogenetic context requires that the group under study has radiated extensively and that the phylogenetic relationships are relatively well understood. Although piranhas and their close relatives have undergone moderate radiation, their taxonomy, particularly at the species level, is still fluid and phylogenetic relationships of serrasalmine fishes are only partly understood. Using morphological characters, Machado-Allison (1985) provided the most current analysis of relationships of the subfamily Serrasalminae (Fig. 1-1). His phylogeny is to genus level only, and its utility for this study is further limited because most species are in the trophically diverse genus *Serrasalmus*.

My study provides information on the diets for nine of the 13 serrasalmine genera. Using data on trophic groupings, I have superimposed my findings onto Machado-Allison's phylogeny (Fig. 8-2) following the methods of Langtimm and Dewsbury (1991). It gives a consistency index of 0.5 suggesting that trophic groupings and intestine length are somewhat consistent with a phylogeny derived from strictly morphological characters. Because much of the variation in trophic characters within the genus *Serrasalmus* was due to the inclusion of *Serrasalmus* cf. *eigenmanni*, if this herbivorous species is not included in the analysis then the consistency index is much higher (i.e., 0.67). Fink (1988) emphasized the need for future studies on piranha ecology and behavior in addition to systematic and phylogenetic analyses. Admittedly, my study on serrasalmine trophic ecology has not answered all the questions. Nevertheless, it will be interesting to see how

the conclusions drawn here fare when they are re-evaluated in light of a well understood phylogeny of the piranhas.

Fig. 8-2. Diets and intestine length mapped onto the proposed phylogeny of Machado-Allison (1985) for genera of the subfamily Serrasalminae. The four piranha genera are highlighted. Orinoco taxa not examined during this study are not included in tree. Jv = juvenile trait; ad = adult trait.


Piscivores
Fin eaters (jv)
Fin eaters (ad)
Scale eaters
Herbivores
Long Intestine
?
?
Piaractus
Mylossoma
Myleus
Metynnis
Catoprion
Pygopristis
Pygocentrus
Pristobrycon
Serrasalmus
Piranhas
= Present in all species
= Variable among species
= Absent in all species

APPENDIX A
MATERIAL EXAMINED

Specimens examined are deposited at the Museo de Ciencias Naturales (MCNG) at UNELLEZ, Guanare, Venezuela, and the Florida Museum of Natural History (UF), Gainesville, Florida. Catalogued specimens are designated by MCNG or UF numbers and uncataloged specimens by field collection numbers (PIMA, DCT or LN). Total number of fish in that series and number of specimens in which gut contents were examined, or intestine measured, is given in parentheses. Small juveniles (jv) are specimens less than 20 mm Standard Length.

Pristobrycon striolatus

Llanos

Apure River drainage: Caño Maporal.-1980: MCNG 9102 (1-0); MCNG 11373 (1-0). 1981: MCNG 9178 (2-0); MCNG 10127 (1-0); MCNG 10247 (6-3); MCNG 11371 (8-5); MCNG 11372 (5-3). 1983: MCNG 10073 (2-1). 1984: MCNG 11347 (6-2); MCNG 11360 (5-1); MCNG 15736 (1-1?). 1985: MCNG 11511 (2-1). 1989: MCNG 19454 (1-1).

Cinaruco River drainage: 1986: MCNG 1793 (1-1). 1987: MCNG 17157 (4-4). 1989: MCNG 21805 (1-1); MCNG 20018 (1-1);

Capanaparo River drainage: 1989: MCNG 20283 (4-4);

Other: 1987: MCNG 17387 (2-2).

Upper Orinoco

Ventuari River drainage: 1989: MCNG 22054 (38jv-38).

Mavaca River drainage: 1991: MCNG 25335 (1-1); Ocamo River drainage: 1990: MCNG 22249 (4-4)

Pristobrycon sp.

Upper Orinoco

Atabapo River drainage: 1989: MCNG 21757 (5-5) (note: these five specimens will be paratypes and divided among several museums, MCNG 21757 [2-2], MBUCV # [1-1], and UMMZ # [2-2]).

Pygocentrus caribe

Llanos

Apure River drainage: UNELLEZ module.-1979: MCNG 3547 (1-1); MCNG 7686 (1-1); MCNG 8313 (4-4); MCNG 8342 (1-0); MCNG 9421 (2-2). 1980: MCNG 1776 (1-1); MCNG 4440 (1-1); MCNG 5899 (8-7); UF 37063 (2-0). 1981: MCNG 1996 (6-0); MCNG 2036 (5-5); MCNG 2076 (2-2); MCNG 2160 (7-7); MCNG 2166 (7-7); MCNG 2188 (5-5); MCNG 2215 (1-1); MCNG 2298 (2-2); MCNG 2357 (4-4); MCNG 2379 (25-25); MCNG 2461 (4-4); MCNG 2482 (1-1); MCNG 3693 (2-2); MCNG 3728 (3-3); MCNG 3754 (1-1); MCNG 3842 (3-3); MCNG 3873 (1-1); MCNG 3888 (9-9); MCNG 4006 (3-3); MCNG 4023 (145-30); MCNG 4049 (13-7,6jv); MCNG 4058 (2-2); MCNG 4074 (3-1,2jv); MCNG 4119 (7-7); MCNG 4135 (6-6); MCNG 4153 (47-47); MCNG 4168 (1-1); MCNG 4200 (2-2); MCNG 4217 (2-2); MCNG 4284 (3-3); MCNG 4309 (2-2); MCNG 4491 (1-1); MCNG 4557 (2-2); MCNG 4689 (2-2); MCNG 4715 (1-1); MCNG 4737 (1-1); MCNG 4757 (2-2); MCNG 4777 (1-1); MCNG 4796 (1-1); 4901 (7-7); MCNG 4925 (5-5); MCNG 5030 (2-2); MCNG 5168 (1-1); MCNG 7881 (57-57?);

MCNG 10418 (2-1,1jv); MCNG 10419 (20-19,1jv); DCT 81-157 (2-1); DCT 81-159 (2-2); DCT 81-160 (20-20); PIMA 18-25 (5-4); PIMA 18-26 (1-1); PIMA 18-27 (6-6); PIMA 18-30 (3-3); PIMA 18-33 (5-5); PIMA 18-36 (7-7); PIMA 18-37 (1-1); PIMA 18-44 (4-4); PIMA 18-46 (7-6); PIMA 18-49 (1-1); PIMA 18-78 (1-1); PIMA 18-90 (14-14); PIMA 18-91 (1-1); uncatalogued student collection (11-10). 1982: MCNG 5075 (1-1); PIMA 18-96 (2-2); PIMA 18-98 (3-3); PIMA 18-99 (4-4). 1983: MCNG 10322 (77-71). 1984: MCNG 10709 (18-18); MCNG 11325 (72-14); 11367 (4-4?); LN 84-7 (14-14); LN 84-8 (8-8); LN 84-76 (71-55?); DCT 84-13 (7-7). 1988: LN 88-23 (12-12); LN 88-24 (13-13); LN 88-26 (43-43); LN 88-27 (17-17); LN 88-28 (11-11); LN 88-29 (11-11); LN 88-30 (16-16). 1989: LN 89-171 (5-2); LN 89-170 (6-6); LN 89-173 (1-1); LN 89-176 (9-9).

Other: MCNG 20751 (7-7); MCNG 8790 (1-1?).

Juveniles less than 20 mm SL.tentatively identified as *P. caribe*. UNELLEZ module.-1981: MCNG 3949 (59-27jv); MCNG 3956 (21-20jv); MCNG 4006 (2-2); MCNG 4023 (145-29jv); MCNG 4049 (13-6jv); MCNG 4074 (3-2jv); MCNG 4075 (1-1); MCNG 4119 (7-3); MCNG 4135 (5-1jv); MCNG 4258 (1-1); MCNG 7881 (57-24jv); MCNG 10418 (2-1jv); MCNG 10419 (20-1jv); MCNG 10424 (1-1).

Upper Orinoco

Ventuari River drainage: .1989: MCNG 22974 (2-2); MCNG 22247 (1-1); LN 89-166 (2-2); LN 89-167 (2-2).

Ocamo River drainage: .1990: MCNG 22269 (2-2); MCNG 22295 (2-2); LN 90-20 (1 1).

Pygopristis denticulatus

Llanos

Apure River drainage: 1981: MCNG 3243 (3-1); UF 36177 (1-0).

Cinaruco River drainage: 1987: MCNG 17157 (4-0?); 1989: MCNG 20018 (2-2); MCNG 20110 (1-1).

Capanaparo River drainage: 1989: MCNG 21885 (4-4); MCNG 17776 (3-3); UF 84183 (1-1).

Upper Orinoco

Venturari River drainage: 1981: MCNG 7874 (2-0);

Atabapo River drainage: 1989 MCNG 21881 (1-1);

Mavaca River drainage: 1991: LN 91-19 (33-9); LN 91-45 (47-15).

Serrasalmus altuvei

Llanos

Apure River drainage: UNELLEZ module.-1979: MCNG 9147 (1-1). 1981: MCNG 3619 (4-4). 1984: MCNG 10713 (5-5). 1985: MCNG 12470 (1-0). Caño Maporal.-1981: MCNG 9356 (1-0); MCNG 11018 (1-0); UF 31859 (2-0). 1983: MCNG 10075 (2-0). 1988: MCNG 21241 (1-1).

Upper Orinoco

Matacuni River drainage: 1990: MCNG 22126 (3-0); MCNG 22417 (1 1).

Mavaca River drainage: 1991: MCNG 25336 (7-7); MCNG 25410 (1-1).

Serrasalmus elongatus

Llanos

Apure River drainage: UNELLEZ module.-1980: MCNG 5902 (2-1). 1981: MCNG 2044 (1-1); MCNG 4560 (1-1); MCNG 4736 (1-1). 1984: MCNG 10711 (9-8). 1985: MCNG 11382 (13-13); MCNG 11539 (2-2). 1989: MCNG 23139 (1-1); MCNG 23156 (1-1); MCNG 23179 (1-1); MCNG 23164 (7-7); MCNG 23386 (1-1); MCNG 23169 (9-9). 1990: MCNG 23384 (2-2). Caño Maporal.- 1980: MCNG 6067 (3-2);

MCNG 9101 (2-1). 1981: MCNG 11015 (2-2); UF 31858 (1-0); UF 77722 (1-0). 1984: MCNG 11361 (8-4); MCNG 11350 (1-1) 1988: MCNG 21242 (2-2). Caño Caicara: 1990: MCNG 23382 (3-3). Other.-1979: MCNG 1193 (1-1); MCNG 9683 (2-2); MCNG 12588 (1-1).

Capanaparo River drainage: 1989: MCNG 20229 (1-0).

Serrasalmus cf. *eigenmanni*

Llanos

Cinaruco River drainage: 1989: MCNG 21380 (1-1); MCNG 20156 (2 2).

Upper Orinoco

Ventuari River drainage: 1989: MCNG 22116 (1-1).

Ocamo River drainage: 1990: MCNG 22415 (1-1); MCNG 22410 (1-1); MCNG 22260 (8-8); MCNG 22287 (1-1); MCNG 22289 (1-1); MCNG 22290 (2-2); MCNG 22250 (3-3); MCNG 22406 (4-4).

Matacuni River drainage: 1990: MCNG 22125 (5-5); MCNG 22129 (9 9).

Orinoco main stem: 1990: MCNG 21850 (1-1).

Mavaca River drainage: 1991: MCNG 25409 (4-4); MCNG 25361 (2-2); MCNG 25364 (4-4); MCNG 25337 (3-3).

Other

Caura River drainage: 1989: MCNG 21047 (3-3); ;MCNG 21593 (3-3); MCNG 21929 (6-6).

Serrasalmus irritans

Llanos

Apure River drainage: UNELLEZ module.-1979: MCNG 7685 (4-4); MCNG 8409 (1-1); MCNG 9443 (2-2). 1980: MCNG 4439 (1-1); MCNG 5901 (13-13). 1981:

MCNG 1995 (6-6); MCNG 2046 (28-28); MCNG 2122 (6-6); MCNG 2162 (4-4); MCNG 2189 (3-3); MCNG 2216 (2-2); MCNG 2336 (1-1); MCNG 2359 (9-9); MCNG 2377 (15-15); MCNG 3645 (1-1); MCNG 3729 (6-6); MCNG 3843 (1-1); MCNG 3889 (1-1); MCNG 3984 (1-1); MCNG 4092 (3-3); MCNG 4154 (2-2); MCNG 4166 (7-7); MCNG 4199 (4-4); MCNG 4218 (1-1); MCNG 4233 (1-1); MCNG 4308 (4-4); MCNG 4341 (3-3); MCNG 4543 (1-0); MCNG 4558 (2-2); MCNG 4583 (1-1); MCNG 4688 (2-2); MCNG 4735 (1-1); MCNG 4776 (1-1); MCNG 4795 (1-1); MCNG 4927 (1-1); MCNG 4974 (20-20); UF 36153 (2-0); UF 77721 (1-0). 1982: MCNG 6325 (1-1). 1984: MCNG 10712 (50-50); MCNG 11324 (2-2); MCNG 11364 (31-31); MCNG 11366 (1-1); MCNG 11370 (1-1); LN 84-8 (1-0); DCT 84-68 (4-4). 1985: MCNG 11383 (17-17); MCNG 11540 (1-0?); MCNG 12471 (6-5). 1989: MCNG 23387 (17-9); MCNG 23134 (6-6); MCNG 23141 (14-7); MCNG 23151 (6-1). 1990: MCNG 23385 (8-8). Caño Caicara: 1989: LN 89-22 (1-1).

Serrasalmus manueli

Llanos

Cinaruco River drainage: 1982: MCNG 5629 (3-3); 1986: MCNG 17954 (1-1). 1987: MCNG 17156 (8-8). 1989: MCNG 22185 (2-2); MCNG 20180 (2-2); MCNG 21764 (8-8); MCNG 21759 (2-2).

Capanaparo River drainage: 1989: MCNG 20064 (1-1).

Upper Orinoco

Sipapo River drainage: 1989: MCNG 21972 (6-6); LN 89-71 (4-4); LN 89-61 (1-1).

Atabapo River drainage: 1989: MCNG 21957 (6-6); MCNG 21795 (5-5); MCNG 22023 (1-1); MCNG 21889 (2-2); MCNG 21890 (1-1); MCNG 22019 (2-2); MCNG

21957 (6-6); MCN G 22020 (1-1); MCNG 21795 (5-5); MCNG 21966 (6-6); LN 89-153 (3-3); LN 89-154 (2-2); LN 89-161 (4-4); LN 89-165 (16-16).

Ventuari River drainage: 1989: MCNG 21969 (3-3); MCNG 21837 (2-2); MCNg 22128 (2-2); MCNG 21972 (1-1); MCNG 21982 (1-1); MCNG 21980 (2-2); MCNG 21969 (3-3); MCNG 22022 (5-5); MCNG 22115 (1-1); Small juveniles tentatively identified as *Serrasalmus manueli*: MCNG 22053 (5-5jv).

Orinoco main stem: 1989: LN 89-92 (1-1). 1990: MCNG 21849 (2-2). 1991: MCNG 25408 (3-3); MCNG 25396 (3-3); LN 91-50 (1-0).

Serrasalmus medinai

Llanos

Apure River drainage: UNELLEZ module.-1979: MCNG 7684 (1-1); MCNG 8408 (1-1); MCNG 11311 (1-1). 1980: MCNG 5900 (16-16). 1981: MCNG 2124 (4-4); MCNG 2165 (1-1); MCNG 2285 (2-2); MCNG 2299 (1-1); MCNG 2358 (3-3); MCNG 2378 (8-8); MCNG 3887 (1-1); MCNG 3918 (1-1); MCNG 4167 (1-1); MCNG 4340 (1-1); MCNG 4559 (2-2); MCNG 4778 (2-2); MCNG 4881 (1-1); MCNG 4926 (4-4); MCNG 4975 (4-4); MCNG 10421 (1-1); MCNG 10422 (1-1); UF 31458 (1-0); UF 36156 (3-0). 1984: MCNG 10710 (20-20); MCNG 11365 (1-1). 1985: MCNG 11384 (21-21); MCNG 12472 (3-3); MCNG 12561 (6-6). 1989: MCNG 23171 (7-7); MCNG 23142 (5-5); MCNG 23152 (5-5); MCNG 23157 (4-4); MCNG 23162 (1-1); MCNG 23155 (1-1); LN 89-20 (1-1). Caño Maporal.-1980: MCNG 9099 (1-1). 1981: MCNG 10126 (1-1); MCNG 10244 (2-2); MCNG 11017 (1-0). 1983: MCNG 10072 (1-1). 1984: MCNG 11351 (2-0); MCNG 12562 (1-1). Other.-1979: MCNG 9684 (14-6); MCNG 9751 (1-1). Caño Caicara: 1990: LN 90-62 (2-2).

Serrasalmus rhombeus

Llanos

Apure River drainage: UNELLEZ module.-1979: MCNG 8267 (1-1); MCNG 8314 (3-3). 1981: MCNG 4137 (1-1); MCNG 10420 (1-1); MCNG 10423 (1-1); MCNG 10464 (1-1); MCNG 11330 (1-1); MCNG 11331 (1-1); (1-1); DCT 81-157 (3-3). 1984: MCNG 11345 (1-1); MCNG 11368 (1-1); MCNG 11377 (1-1). 1988: 19070 (1-1); LN 89-12 (1-1). 1989: MCNG 23389 (2-2). Caño Maporal.-1981: MCNG 10168 (1-1); MCNG 10246 (1-1); MCNG 10288 (7-7); UF 77723 (2-0). 1984: MCNG 11362 (7-6); MCNG 11348 (1-1); MCNG 11376 (2-2). Other.-1979: MCNG 9752 (13-4). 1984: MCNG 1927 (1-1); MCNG 11378 (4-4); MCNG 12933 (6-6).

Upper Orinoco

Orinoco main stem: 1989: MCNG 22503 (2-2); LN 89-92 (1-1). 1991: MCNG 25397 (1-1)

Ventuari River drainage: 1989: MCNG 22021 (1-1); MCNG 21970 (1-1); MCNG 21981 (1-1); MCNG 21968 (3-3); LN 89-111 (5-5); MCNG 21926 (1-1); MCNG 22021 (1-1); MCNG 22503 (2-2);

Matacuni River drainage: 1990: MCNG 22507 (3-3); MCNG 22127 (14-14);

Ocamo River drainage: 1990: MCNG 22109 (1-1); MCNG 22102 (1-1); MCNG 22114 (5-5); MCNG 22130 (1-1); MCNG 22131 (1-1); MCNG 22270 (3-3); MCNG 22294 (2-2); MCNG 22411 (1-1); MCNG 22412 (4-4); MCNG 22416 (5-5); MCNG 22420 (1-1); MCNG 22251 (1-1); MCNG 22261 (2-2); MCNG 22923 (1-1); LN 90-12 (5-5); LN 90-14 (6-6); LN 90-19 (1-1); LN 90-21 (1-1); LN 90-22 (1-1); LN 90-26 (2-2); LN 90-27 (3-3); LN 90-33 (1-1); LN 90-42 (7-7); LN 90-37 (4-4); LN 90-38 (2-2); LN 90-45 (2-2); LN 90-46 (2-2); LN 90-49 (1-1);

Mavaca River drainage: 1991: MCNG 25365 (1-1).

Other Serrasalmine Fishes

Catoprion mento

Llanos: UNELLEZ module.-1979: MCNG 9422 (2-2). 1980: MCNG 4428 (1-1); MCNG 5897 (10-10); UF 37061 (1-0). 1981: MCNG 1986 (1-1); MCNG 2055 (5-5); MCNG 2179 (1-1); MCNG 4866 (1-1). 1984: MCNG 10708 (31-31). 1985: MCNG 11385 (78-5). Caño Maporal.-1980: MCNG 6070 (6-6); MCNG 9111 (8-8). 1981: MCNG 5765 (5-5); MCNG 7655 (6-6); MCNG 9179 (1-1); MCNG 9358 (1-1); MCNG 10219 (1-1); UF 77720 (1-0). 1982: MCNG 7046 (3-3). 1983: MCNG 10071 (13-13). 1984: MCNG 11374 (2-2); MCNG 11375 (1-1). 1989: MCNG 23388 (1-1)

Upper Orinoco: Ocamo River drainage: 1990: MCNG 23415 (2-2). Mavaca River drainage: 1991: MCNG 25403 (1-1); MCNG 25404 (1-1); MCNG 25362 (1-1); MCNG 25353 (1 1); UF 85217 (1-1).

Metynnis spp.

Llanos: Apure River drainage: 1984: LN 84-7 (1-1). 1985: MCNG 11508 (17-3). 1989: MCNG 23174 (6-1); MCNG 23145 (3-1); MCNG 23178 (1-1); MCNG 23161 (1-1).

Upper Orinco: Mavaca River drainage: 1991: MCNG 25333 (1-1); MCNG 25360 (1-1); MCNG 25411 (2-2); MCNG 25363 (1-1); LN 91-19 (2-1); LN 91-45 (1-1).

Myleus asterias

Upper Orinoco: Mavaca River drainage: 1991: UF 85212 (2-0); MCNG 25334 (11-2). Matacuni River drainage: 1990: MCNG 23381 (1-1); MCNG 23379 (1-1); Ocamo River drainage: 1990: MCNG 23380 (8-8); MCNG 22288 (5-4); MCNG 22412 (4-3); MCNG 22413 (1-1); MCNG 22408 (2-2); MCNG 23416 (16-14).

Myleus schomburgkii

Llanos: Capanaparo River drainage: 1989: MCNG 20067 (2-2); MCNG 20086 (3-3). Cinaruco River drainage: 1989: MCNG 20173 (1-1). Riecito River drainage: 1982: MCNG 6209 (2-2).

Upper Orinoco: Orinoco main stem: 1991: MCNG 25399 (1-1). Ventuari River drainage: 1989: MCNG 22885 (2-2). Atabapo River drainage: LN 89-162 (2-2). Ocamo River drainage: 1990: MCNG 22407 (1-1); Mavaca River drainage: MCNG 25401 (1-1) Casiquiare: 1985: MCNG 12354 (1-1).

Myleus torquatus

Upper Orinoco: Orinoco main stem: 1991: MCNG 25398 (2-2); LN 91-3 (4-4). Ocamo River drainage: 1990: MCNG 23378 (1-1). Ventuari River drainage: 1989: MCNG 22884 (4-3). Mavaca River drainage: 1991: MCNG 25423 (14-14); UF 85213 (2-2).

Myleus sp.

Upper Orinoco: Atabapo River drainage: 1989: LN 89-162 (2-2).

Mylossoma duriventrus.

Llanos: Apure River drainage: 1981: MCNG 2091 (1-1). 1984: MCNG 17154 (1-1).

Piaractus brachypomus

Upper Orinoco: Sipapo River drainage: 1989: LN 89-63 (1-1).

APPENDIX B
STATISTICAL ANALYSES

Analysis of Covariance (ANCOVA)

Following are the results of ANCOVA comparing intestine length and standard length of different combinations of piranha species. Analysis carried out using Type III sum of squares of SuperANOVA computer program on a MacIntosh SE/30 computer. Data were not transformed.

Table B-1. ANCOVA of standard length (SL), with intestine length (IL) as dependent variable, comparing three piranha species from upper Orinoco: *Serrasalmus manueli* (n = 60), *S. rhombeus* (n = 70), and *S.* cf. *eigenmanni* (n = 32).

Source	df	Sum of squares	Mean squares	F-value	P-Value
Species	2	6863.142	3431.571	1.570	0.2112
SL	1	887772.922	887772.922	406.273	0.0001
Species x SL	2	63119.741	31559.870	14.443	0.0001*
Residual	156	340885.717	2185.165		

*Conclude that slopes of regression lines are different.

Table B-2. ANCOVA of standard length (SL) with intestine length (IL) as dependent variable comparing Upper Orinoco *Serrasalmus manueli* (n = 60) and *S. rhombeus* (n = 70).

Source	df	Sum of squares	Mean squares	F-value	P-Value
Species	1	574.649	574.649	0.288	0.5924
SL	1	1923573.822	1923573.822	964.479	0.0001
Species x SL	1	6466.875	6466.875	3.242	0.0741*
Residual	126	251296.649	1994.418		

*Conclude that slopes of regression lines are not different at 0.05 level of significance, therefore eliminate interaction effect (see Table B-3) to see if y-intercept is the same..

Table B-3. ANCOVA of standard length (SL) with intestine length (IL) as dependent variable comparing Upper Orinoco *Serrasalmus manueli* (n = 60) and *S. rhombeus* (n = 70) eliminating interactive effect (i.e., adjusting for differences in SL).

Source	df	Sum of squares	Mean squares	F-value	P-Value
Species	1	68775.973	68775.973	33.886*	0.0001*
SL	1	1922891.270	1922891.270	947.408	0.0001
Residual	127	257763.523	2029.634		

*Adjusting for differences in SL, reject null hypothesis and conclude that y-intercepts are different, therefore the IL of the two species differ significantly (F = 33.89, P = 0.0001).

Table B-4. ANCOVA of standard length (SL) with intestine length (IL) as dependent variable comparing Upper Orinoco *Serrasalmus manueli* (n = 60) and *S.* cf. *eigenmanni* (n = 32).

Source	df	Sum of squares	Mean squares	F-value	P-Value
Species	1	6822.825	6822.825	3.024	0.0856
SL	1	547308.446	547308.446	242.538	0.0001
Species x SL	1	48373.729	48373.729	21.437*	0.0001*
Residual	88	198579.446	2256.585		

*Conclude that slopes of regression lines are different, and that the IL/SL ratio of *S.* cf. *eigenmanni* is significantly greater.(F = 21.44, P = 0.0001).

Table B-5. ANCOVA of standard length (SL) with intestine length (IL) as dependent variable comparing Upper Orinoco *Serrasalmus rhombeus* (n = 70) and *S.* cf. *eigenmanni* (n = 32).

Source	df	Sum of squares	Mean squares	F-value	P-Value
Species	1	4463.807	4463.807	1.886	0.1727
SL	1	506164.993	506164.993	213.908	0.0001
Species x SL	1	61742.334	61742.334	26.093*	0.0001*
Residual	98	231895.339	2366.279		

*Conclude that slopes of regression lines are different, and that the IL/SL ratio of *S.* cf. *eigenmanni* is significantly greater.(F = 26.09, P = 0.0001).

Table B-6. ANCOVA of standard length (SL) with intestine length (IL) as dependent variable comparing Upper Orinoco *Serrasalmus manueli* (n = 60) and low Llanos *S. manueli* (n = 20).

Source	df	Sum of squares	Mean squares	F-value	P-Value
Species	1	1857.851	1857.851	0.815	0.3696
SL	1	1147080.511	1147080.511	503.084	0.0001
Species x SL	1	1527.190	1527.190	0.670	0.4157*
Residual	76	173287.427	2280.098		

*Conclude that slopes of regression lines are not different at 0.05 level of significance, therefore eliminate interaction effect (see Table B-6) to see if y-intercept is the same..

Table B-7. ANCOVA of standard length (SL) with intestine length (IL) as dependent variable comparing Upper Orinoco *Serrasalmus manueli* (n = 60) and low Llanos *S. manueli* (n = 20) while eliminating interactive effect (i.e., adjusting for differences in SL).

Source	df	Sum of squares	Mean squares	F-value	P-Value
Population	1	336.248	336.248	0.148*	0.7014*
SL	1	1481368.833	1481368.833	652.493	0.0001
Residual	127	174814.617	2270.320		

*Adjusting for differences in SL, reject null hypothesis and conclude that y-intercepts are different, therefore the IL of the two species differ significantly (F = 33.89, P = 0.0001).

Mann-Whitney *U* Test

Following are the results of one-tailed Mann-Whitney U tests comparing the degree of herbivory of piranha populations from the low Llanos to those from the upper Orinoco. Comparisons are made using results of percent adjusted volume ($\%V_a$), percent dominance (%D), and percent frequency of occurrence (%O), based on specimens ≥ 80 mm SL (combining information on the two largest size classes for each species, 80-159 mm SL and ≥ 160 mm SL). Specimens with empty stomachs were not figured into the calculations. Number of specimens by species is given in Table 6-9.

Table B-8. Percent adjusted volume ($\%V_a$) of plant material in piranhas (≥ 80 mm SL) as associated with the low Llanos and upper Orinoco.

	Low Llanos	Upper Orinoco
Taxon	$\%V_a$	$\%V_a$
Pristobrycon sp.	-	100.0
Pristobrycon striolatus	41.0	73.0
Pygocentrus caribe	6.7	11.0
Pygopristis denticulatus	50.0	100.0
Serrasalmus altuvei	0	0
S. cf. *eigenmanni*	25.0	70.0
S. manueli	0	26.0
S. rhombeus	11.9	2.0
S. elongatus	3.6	-
S. irritans	5.0	-
S. medinai	2.9	-

Table B-9. Percent dominance (%D) of plant material in piranhas (≥ 80 mm SL) as associated with the low Llanos and upper Orinoco.

	Low Llanos	Upper Orinoco
Taxon	%D	%D
Pristobrycon sp.	-	100.0
Pristobrycon striolatus	50.0	80.0
Pygocentrus caribe	11.2	33.3
Pygopristis denticulatus	66.7	100.0
Serrasalmus altuvei	0	0
S. cf. *eigenmanni*	33.3	68.2
S. manueli	0	27.0
S. rhombeus	12.5	1.7
S. elongatus	4.0	-
S. irritans	8.6	-
S. medinai	6.0	-

Table B-10. Percent frequency of occurrence (%O) of plant material in piranhas (≥ 80 mm SL) as associated with the low Llanos and upper Orinoco.

	Low Llanos	Upper Orinoco
Taxon	%O	%O
Pristobrycon sp.	-	100.0
Pristobrycon striolatus	80.0	100.0
Pygocentrus caribe	34.1	50.0
Pygopristis denticulatus	66.7	100.0
Serrasalmus altuvei	28.6	22.2
S. cf. *eigenmanni*	66.7	81.8
S. manueli	8.3	43.2
S. rhombeus	25.0	15.5
S. elongatus	32.0	-
S. irritans	18.6	-
S. medinai	26.0	-

Table B-11. One-tailed Mann-Whitney U test results testing the prediction that forest populations fed more on plant material than their savanna counterparts. N_1 = number of species from upper Orinoco; N_2 = number of species from low Llanos.

Diet Measure	N_1	N_2	U	Mean	SD*	*z* value*	P
$\%V_a$	8	10	23	40	11.22556	- 1.514402	0.0655
%D	8	10	22.5	40	11.21973	- 1.559752	0.0594
%O	8	10	23	40	11.21556	- 1.514402	0.0655

*Corrected for ties

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BIOGRAPHICAL SKETCH

Leo G. Nico was born on December 25, 1954, to Frank and Teresa Nico in East St. Louis, Illinois. He grew up in a small Illinois town where he developed an early interest in biology and natural history. One year after graduating from high school, he entered Southern Illinois University at Edwardsville (SIUE), majoring in biology. He was awarded a Bachelor of Arts degree with honors in 1979. Forsaking plans to enter the Peace Corps, he became a graduate student at SIUE to work under Dr. Jamie E. Thomerson on the ecology and natural history of South American annual fishes. Field work for his master's degree was done in the Orinoco River basin of Venezuela during the rainy season of 1980. Concurrent with his graduate studies, he did a study of the breeding birds of the lower Kaskaskia River, under a contract with the Illinois Department of Conservation. He also held a temporary position with the U.S. Army Corps of Engineers as a fishery biologist in their Environmental Analysis Section. After receiving his M.Sc. degree in 1982, he worked one more year for the Federal government, still harboring plans to work in the tropics as a Peace Corps volunteer. But, once again, his plans were curtailed upon receiving an invitation from Professor Donald Taphorn to help him in a study of the fishes of the Apure River basin in Venezuela. As a result, he spent from November 1983 to July 1985 in Venezuela.

In 1985, he moved to Gainesville after being accepted into the Ph.D. program in the Department of Zoology at the University of Florida. As part of his graduate studies, he did additional field work in South America, spending two months in Brazil in 1986, and approximately two years of field work in Venezuela from 1988 to1991.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Horst O. Schwassmann, Chair
Professor of Zoology

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December, 1991

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